

Peculiarities of the butterfly fauna of South-East Sulawesi

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Abstract: The complex structure and geological history of Sulawesi renders this island an ideal object for zoogeographical studies on butterflies and their evolution. Based on the faunal composition and species endemism, Sulawesi can be subdivided into several regions (Vane-Wright & de Jong 2003). Unfortunately, the state of knowledge concerning the butterfly fauna differs substantially between these regions, East and SE Sulawesi being particularly under-represented. Therefore, I will focus here on the less explored southeastern peninsula, Sulawesi Tenggara, and try to carve out some peculiarities of this region with respect to butterflies. SE Sulawesi harbours several unique species and subspecies such as *Lohora umbrosa* and *Zethera incerta tenggara* and also species which are extremely rare on Sulawesi such as *Semanga helena*, *Deudorix loxias* and *Euthalia aconthea*. On the other hand, a number of species occurring in other parts of Sulawesi are missing in the southeast: *Atrophaneura dixonii* Grose-Smith, 1901, *Charaxes mars* Staudinger, 1885 and *Cyrestis heracles* Staudinger, 1896 are examples. A notable feature in SE Sulawesi of many butterfly species from different families is the trend for darker wing coloration compared to populations from other parts of the island. It is attempted here to quantify this phenomenon and to provide respective, reproducible methods for its analysis. This has been done for example for several species of the Pierid genus *Eurema* Swainson, 1821 and for the Nymphalid species *Cyrestis strigata* Felder et Felder, 1867, *Neptis ida* Moore, 1858 and *Lexias aeetes* Hewitson, 1861. The above mentioned peculiarities will be finally discussed in a zoogeographic context.

Key words: Sulawesi, Sulawesi Tenggara, Pieridae, Lycaenidae, Nymphalidae.

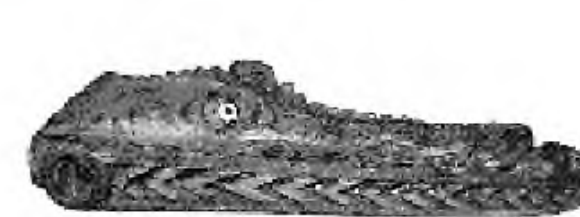
Introduction

The butterfly fauna of Sulawesi was intensely studied in the 19th and early 20th centuries, connected with names such as the famous Alfred Russel Wallace and Ludwig Martin. After a gap of many decades, more comprehensive recent investigations were performed in 1978 and 1985 by “Operation Drake” as part of a world-wide program organized by the Scientific Exploration Society (Blashford-Snell 1981) and by “Project Wallace” organized by the Royal Entomological Society of London (Knight 1988; Knight & Holloway 1990). However, these explorations were restricted to relatively small parts of the large island, i.e. Morowali district in Central Sulawesi and Bogani Nani Wartabone (former Dumoga-Bone) in North Sulawesi, respectively. Hence, large areas of Sulawesi remained, and remain, largely unexplored, such as the southeastern and eastern peninsula as already mentioned by Vane-Wright & de Jong (2003). The author’s own investigations over the last 20 years, of the less known butterfly fauna of the southeastern part of Sulawesi, were undertaken

to fill the gaps of knowledge. Successively, these investigations have brought forward the entomofaunistic peculiarities of this part of the island and lead to the notion that it forms a specific biogeographic entity within Sulawesi, together with the large south-eastern offshore islands such as Buton and Muna (Roos 1993, 1995, 2000, 2005). The following aspects concerning the butterfly fauna of Southeast Sulawesi (SE Sulawesi) will be treated here: the occurrence of rare or unique species or subspecies, first records for SE Sulawesi, the obvious absence of species which are present in other parts of the island and the parallel evolution of certain character traits in different species. Finally, zoogeographic aspects such as the relationship between SE Sulawesi and the large adjacent islands Buton and Muna will be discussed.

Materials and methods

For the analysis of wing patterns and for morphometric determinations the FIJI software



was used (Abramoff et al. 2004). The functions 'straight line' and 'polygon selection' were applied to determine lengths and areas, respectively. The 'rectangular selection' was used to define areas for intensity measurements. Absolute length and area values in mm and mm² were normalized to account for differences in the size of butterflies. For normalization, forewing length or total forewing area are used, for example. Other suitable parameters will be indicated. Calculations were done with Microsoft Excel. For the graphical presentation of bar diagrams, box plots and functions GraphPad Prism was used. Student's T-test was applied to calculate statistical significance.

Particular butterfly species and subspecies from Sulawesi Tenggara

This section discusses the occurrence of species and subspecies which are either generally rare and very locally distributed on Sulawesi, or are specific / endemic for the southeast peninsula.

Rare and new encounters for Sulawesi Tenggara

***Deudorix loxias* Hewitson, 1863 (Lycaenidae)** (Plate 85 figs 1,4)

D. loxias - often misspelled as *loxius* - is an endemic Lycaenid of Sulawesi. It appears to be very rare on the entire island as mentioned by Röber (1939). This notion also reflects the current picture as there are only few specimens in museum collections and there is little known on the distribution, biology and ecology of the species (Muller & Tennent 2011). Recently, *D. loxias* has been recorded from Buton island to the south of Sulawesi Tenggara. Now, I can add 'Kolaka' as a new locality in the latter province where I found this species in 2015. Altogether 3 female specimens were sighted (Plate 85 figs 1,4) in March 2015 within dense and deep forest about 8 km east of Kolaka at an altitude of roughly 400 m. The specimens were observed within a small area on a transect of about 50 m and were not seen elsewhere in the surrounding area. They were flying 1 to 2 m above the ground and settled on leaves. In summary, the occurrence of *D. loxias* in SE Sulawesi has been proven for the first time. The species belongs to the rarest butterflies of Sulawesi Tenggara and also of entire Sulawesi. *D. loxias* appears to form very local populations restricted to small patches within the forest. More observations are needed to find out the peculiarities of these patches considering aspects such as micro-climate

and floral composition. It is noted that the Lycaenid *Arhopala argentea* Staudinger, 1888 shows similar distribution behaviour. The species does not occur in the *D. loxias* habitat but inhabits close-by forest areas at altitudes about 50 to 100 m higher. Also for *A. argentea*, more observations are required to define the ecological needs of the species.

***Semanga helena* Röber, 1887 (Lycaenidae)**

S. helena was originally described by Röber (1887) from the Banggai Archipelago, located in the Tomini Bay of East Sulawesi, based on an unstated number of specimens. However, the species appears to be rare on Banggai as well as Peleng, the largest island of the Banggai Archipelago, as neither Nieuwenhuis (1946) nor Detani (1983) could find the species there. The presence of *S. helena* on Sulawesi mainland was shown first time by Tennent (2005) based on 2 specimens which originate from North and Central Sulawesi. A third specimen, a female, was thereafter detected on 01.IV.2009 in SE Sulawesi in the forests about 20 km east of Kolaka (Roos 2016). Thus, the three specimens of *S. helena* known from Sulawesi mainland so far originate from three different locations which are far away from each other. In conclusion, it can be stated that *S. helena* is one of the rarest butterfly species of Sulawesi.

Unfortunately, comprehensive treatments of the entire family Lycaenidae from Sulawesi do not exist. Distribution data for most species are lacking and, generally, little is published on this butterfly group from Sulawesi, an exception being revisions published by Alan Cassidy on the genera *Nacaduba* Moore, 1881 and of the *Lycaenopsis*-group and the tribe Miletini (Cassidy 1990; 1995a; 1995b). Therefore, some further interesting Lycaenidae species will be listed and discussed shortly in the following section. None of these species has been reported before from SE Sulawesi.

***Hypothecia honos* de Nicéville, 1898** (Plate 85 figs 2, 5)

The genus *Hypothecia* Semper, 1890 includes only two species (Fruhstorfer 1912) which are obviously rare (Vane-Wright & de Jong 2003). One of the species, *H. honos*, is endemic for the Sulawesi region and has been described by de Nicéville (1898) from specimens collected by Fruhstorfer in Toli-Toli in North Sulawesi. Röber (1939) mentions the species from North and Central-Sulawesi without giving exact locations. There are no records for SE Sulawesi (Jurriaanse & Lindemans 1920) nor for Southwest Sulawesi (Piepers & Snellen 1878).



In March 2013, I found the species very localized in Porabua (19/20.III) and in Konawendepiha (16/17.III), both places located in the district Uluiwoi. Altogether 5 specimens were recorded. As Sulawesi Selatan is well explored, I suspect that *H. honos* is restricted in the South of Sulawesi to the southeastern peninsula.

***Jamides latimargus* Snellen, 1878**

During altogether nine field trips to SE Sulawesi I recorded this species only once. It was found in the vicinity of Konawendepiha (district Uluiwoi) in March of 2013. The species status of *latimargus* is not clear. Originally the taxon was described by Snellen as *Cupido latimargus* (Piepers & Snellen, 1878) from material which originated from Southwest Sulawesi, namely Amparang, Bonthain, Maros and Takalar. Later, *latimargus* was treated as subspecies either of *J. elpis* Godart, 1824 (Röber 1939) or of *J. alecto* Felder, 1860 (Vane-Wright & de Jong 2003) while Hirowatari (1992) gives it species status as *Jamides latimargus*. D'Abrera (1986) does not at all mention *latimargus*. I will leave the question on the taxonomic status open but follow Hirowatari (1992) as there are substantial differences in wing size and wing colour pattern between *J. latimargus* and *J. alecto*. Interestingly, *Lampides kondulana espada* Fruhstorfer, 1915 was recently recognized as a subspecies of *J. alecto* (Cassidy, 2013). The type material comes from North Sulawesi, Minahassa (Lectotype) and more interestingly also from Southwest-Sulawesi, Bua-Kraeng (paralectotype), from where also *latimargus* was described. The male lectotype figured by Cassidy (2013) is clearly different from the specimen of *J. latimargus* shown here (Plate 85 figs 3, 6). There are no published records for *latimargus*, *alecto* or *elpis* in South-east Sulawesi so that the specimen from Konawendepiha in SE Sulawesi appears to be the only one known so far of *J. latimargus* from that region.

***Jamides snelleni* Röber, 1886**

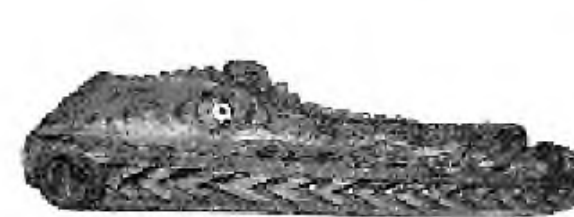
The occurrence of *J. snelleni* in SE Sulawesi has been discussed recently (Roos 2016). The species is endemic for Sulawesi and it is generally rare. Vane-Wright & de Jong (2003) give only South Sulawesi as distribution range for *J. snelleni* although Röber (1939) also mentions Tombuku in East Sulawesi as location. However, there were no previous reports of *J. snelleni* from SE Sulawesi until a single population was discovered there in 2002 in the vicinity of Sambeani, district Abuki (Roos 2016).

***Jamides fractilinea* Tite, 1960** (Plate 85 figs 7, 10)

J. fractilinea is endemic for the Sulawesi region which harbours two subspecies, nominate ssp. *fractilinea* from Sulawesi and ssp. *saraharum* Rawlins, Cassidy, Müller, Schröder et Tennent, 2014 from Mangole Island (Sula Islands) (Rawlins et al. 2014). As there are no definite reports for *J. fractilinea* from Sulawesi Tenggara, the species will be shortly discussed here. The holotype of *J. fractilinea* originates from Makassar in Southwest Sulawesi (Tite 1960). Most of the material further examined by Tite (1960) also comes from this province namely from the following locations: Pic de Bonthain, Maros, Tjamba, Samanga, Lompa Battau and Bua-Kraeng (names spelled as in the original work). In addition one male each from Toli-Toli, North Sulawesi and from Mangole Island were examined. Hirowatari (1992) and Vane-Wright & de Jong (2003) restrict the distribution range of the species to Southwest Sulawesi. I could detect the species at various places and in several years in SE Sulawesi as follows: 20 km East of Kolaka, 12.X.2005, 30 and 31.III.2009, 17. and 20.III.2011, 24.III.2013; Sambeani, 11.X.2002; Porabua, 11.III.2011, 18 and 20.III.2013. At each date, one or sometimes two specimens were recorded making up a total number of twelve only.

***Amblypodia narada* Horsfield, 1829**

The species is widespread in Southeast Asia including islands such as Sumatra, Java, Borneo and the Philippines (Bethune-Baker 1903; Fruhstorfer 1907; D'Abrera 1986). Riley (1922) recognized that *A. narada* also occurs on Sulawesi as he identified a specimen from Makassar among *Amblypodia annetta* Staudinger, 1888 in the collection of BMNH. Based on differences in wing markings he separated it from populations of other islands as ssp. *confusa* Riley, 1922. There is only little further faunistic information regarding *A. narada* from Sulawesi. Fruhstorfer (1907) mentions it from Sula Mangole-Island located in the most eastern part of the Sulawesi region. However, the source of this information remains obscure. Alan Cassidy (2011) figured an image of *A. narada confusa* from Dumoga Bone in North Sulawesi on the internet. In conclusion, only South-west Sulawesi and North Sulawesi can be regarded as assured distribution areas of *A. narada* on Sulawesi based on literature data. There is a new record now from Porabua in SE Sulawesi (12.III.2011, P. Roos). The respective specimen shows the reduced dark blue area on the wing uppersides which is characteristic for ssp. *confusa* (Plate 85 figs 8, 11).



The genus *Dacalana* Moore, 1884

The genus comprises more than 20 different species of which three occur in the Sulawesi region and two on Sulawesi itself, *Dacalana anysis* Hewitson, 1865 and *Dacalana anysides* Röber, 1887. Obviously little is known on the distribution of both species in the different provinces of Sulawesi. The genus *Dacalana* is not mentioned by Jurriaanse & Lindemans (1920) from Sulawesi Tenggara.

Dacalana anysis Hewitson, 1865

While Vane-Wright & de Jong (2003) give Sulawesi generally as the distribution range for *D. anysis*, Röber (1939) restricts this somewhat mentioning only South and North Sulawesi. Originally the species was described from Makassar (Hewitson 1865) and later Holland (1891) lists the species as taken also in Southwest-Sulawesi. The occurrence of *D. anysis* in SE Sulawesi is proven by the specimen shown on plate 85 figs 9 & 12. It was taken in Konawendepiha, district Uluiwoi, on 10.III.2011.

Dacalana anysides Röber, 1887

The species description is founded on a single male taken in Gorontalo which is located in North Sulawesi - not East Celebes as stated by the author (Röber 1887). Its occurrence there was confirmed during Project Wallace by Cassidy (pers. comm.). Ribbe (1926) describes the ssp. *birui* from Kalawara, West-Sulawesi under the name *Camena anysides birui*. The subspecies is distinguished from the nominotypical form by extended blue coloration in particular of the hindwing. Strange to say that the taxon is not considered by subsequent authors, for example Röber (1939), D'Abrera (1986) and Vane-Wright & de Jong (2003). Instead, D'Abrera (1986) figures specimens from the northern part of West-Sulawesi (Palu) under *D. anysides anysides*. There are obviously no published records for *D. anysides* from SE Sulawesi. A single male shown in plate 86 figs 1, 4 was found at the small Silui River close to Porabua on 20.III.2013 and is the only proof of the occurrence of the species in Sulawesi Tenggara.

Arhopala argentea Staudinger, 1888 (Plate 86 figs 2-3, 5-6)

Typical *A. argentea* come from Minahassa in North Sulawesi (Staudinger 1888), and Röber (1939) states that it is rare in that region. In 1897 Grose-Smith described the same species as *Arhopala clarissa* based on material from South Sulawesi (Grose-Smith 1897) so that the distribution area can be summarized as North and South Sulawesi

(Bethune-Baker 1903). Again, there are no published records from SE Sulawesi. In March 2011, a population of *A. argentea* was discovered within montane forest about 20 km east of Kolaka at an elevation of about 500 m. The continuance of the population has been confirmed in 2013 and again in 2015. As already mentioned above (see under *Deudorix loxias*) the species appears to inhabit localized patches within the forest. The ecological reasons for the restriction are not known.

Euthalia aconthea Cramer, 1777 (Nymphalidae)

The discovery of *E. aconthea* in Sulawesi Tenggara in 2002 has been described earlier (Roos 2005). To the best of my knowledge, the specimen of *E. aconthea* found near Kolaka (Plate 86 figs 7-8) is the only one known from SE Sulawesi so far. Only three further specimens have been found in Sulawesi in the Southwest Province (Sulawesi Selatan) (Müller 1994). Outside Sulawesi, *E. aconthea* inhabits a large area in south and south-east Asia (Corbet 1945; Tsukada 1991). Thus, the location at Kolaka forms the most eastern one where the species obviously meets its ecological limits. This concerns also the entire genus *Euthalia* which is represented on Sulawesi by only two species, *E. aconthea* and *E. amanda* Hewitson, 1862. The latter obviously occurs throughout all parts of Sulawesi and also on the Banggai Islands in the east of the Sulawesi region (Tsukada 1991; Vane-Wright & de Jong 2003). The only *Euthalia* species expanding further into the East is *E. amabilis* Staudinger, 1896 which occurs on Sula (Mangole Island), the most eastern outpost of the genus when the Papuan *Euthaliopsis aetion* Hewitson, 1862 is considered phylogenetically distinct from *Euthalia* (see Parsons 1999).

Species or subspecies unique for SE Sulawesi

Zethera incerta tenggara Roos, 1992 (Nymphalidae: Satyrinae)

The genus *Zethera* Felder, 1861 is represented in South-East Sulawesi by a very distinct form which was discovered in 1990 some 20 kilometers east of Kolaka and later tentatively described as a subspecies of *Zethera incerta* Hewitson, 1861 (Roos 1992). The species was formerly believed to be restricted to the northern parts of Sulawesi and, thus, geographically closely connected to its congeneric species inhabiting the Philippine islands. While the latter harbor five different species, only the endemic *Z. incerta* is known from Sulawesi. At the first sighting, the specimens observed in their



habitats in Sulawesi Tenggara were believed to be Danaidae based on the typical gliding flight and on the similar wing pattern. So it was a surprise when the collected specimens turned out to be a *Zethera* species of the Nymphalid subfamily Satyrinae which significantly differs from the nominotypical northern populations as detailed in the original description of *Z. incerta tenggara* by Roos (1992) and demonstrated by figures (Plate 87 figs 1, 3).

The unique subspecies was subsequently also found at Moramo about 75 south of Kendari by K. Willmott in September 2000 during "Operation Wallacea" (<http://www.flmnh.ufl.edu/butterflies/neotropica/sulawesi/checklist.html>). In addition to the type locality about 20 km east of Kolaka, ssp. *tenggara* could also be observed in the vicinity of Sambeani in the mountainous regions to the north of the line Kolaka – Kendari. Field studies at further locations northwards of Sambeani such as Asenua, Tawangga and in particular Porabua could not prove the occurrence of ssp. *tenggara* there. However, a population was discovered recently in Konawendepiha (15.III.2013, P. Roos) which thus constitutes the most northern location from where ssp. *tenggara* is known so far. The exact northern distribution limits and possible contact zones with the nominate subspecies are not known up to now. A specimen from the Luwuk district in East Sulawesi has been assigned to the ssp. *tenggara* and figured, but appears to be intermediate between the nominate form and ssp. *tenggara* with respect to the intensity of yellow coloration and the row of hindwing ocelli (<http://www.neutron.phys.ethz.ch/Lepidoptera/Satyrinae-misc.htm>). More information is needed on the populations in Sulawesi Tengah.

Vane-Wright & Smiles (1975) have discussed mimicry relationships between species of the genus *Zethera* and of the subfamily Danainae. They doubt that there is a definite mimic counterpart for *Z. incerta* as has been suggested by Fruhstorfer (1909) who considers *Ideopsis vitrea* Blanchard, 1853 as a suitable model. While *I. vitrea* only marginally resembles *Z. incerta tenggara* it shows significantly larger congruence in the wing patterns with the northern nominate subspecies *Z. incerta incerta*, as depicted by plate 87 figs 3, 4. On the forewings of both species cells M3, CuA1 and CuA2 are white while light areas closer to the wing margin are yellow coloured. A similar distribution between white and yellow areas is found also on the hindwings. The clear indentations of the brown marginal wing markings on both forewings and hindwings of *Z. incerta* are also mimicked by *I.*

vitrea.

For ssp. *tenggara*, I propose *Ideopsis juvena* Cramer, 1777 (Plate 87 fig. 2) as a possible mimicry partner. It appears to be an efficient model not only based on the wing pattern but also because it is rather abundant in the *Z. incerta tenggara* habitats near Kolaka and Sambeani. In contrast, *Ideopsis vitrea* is less common here. In conclusion, *Z. incerta* obviously exploits two different *Ideopsis* species for its self-protection dependent on the subspecies under consideration.

There are a number of open questions concerning *Z. incerta* and its subspecies *tenggara*:

- (1) Where are the distribution limits for both taxa and where are the contact zones?
- (2) Might ssp. *tenggara* constitute a good species distinct from *Z. incerta*?
- (3) What are the phylogenetic relationships between the two taxa from Sulawesi in relation to the Philippine species?

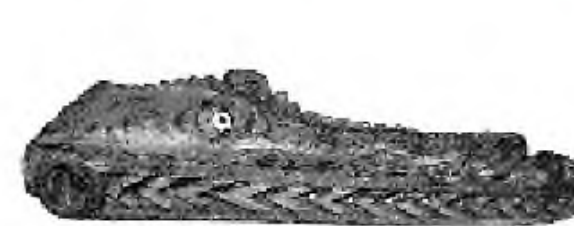
Martin (1929) states that the occurrence of *Z. incerta* is restricted to the northern parts of Sulawesi and that it is missing from the two southern peninsulas. He assumes that the southern distribution limit may run north of the Gulf of Bone. The map of Aoki et al. (1982) additionally excludes the eastern peninsula but includes the northern parts of Sulawesi Selatan although there are no concrete data from the latter area. Only Palopo located at the north-western part of the Bone Gulf is mentioned. Thus, there is a large geographical and knowledge gap between the most northern ssp. *tenggara* populations and the southernmost ssp. *incerta*. Investigation of this 'terra incognita' would reveal

- (1) whether the genus *Zethera* is represented here,
- (2) whether there is a clear-cut division between *incerta* and *tenggara* or
- (3) whether there is a transitional zone with interbreeding populations eventually resulting in clinal variation.

Specimens of *Z. incerta* from South-East Sulawesi generally show darker wing patterns than their counterparts from other areas in Sulawesi, a feature which is shared by numerous other butterfly species as will be shown below. It appears to be characteristic and to be a general trend at least for butterflies of this region.

***Lohora umbrosa* Roos, 1997 (Nymphalidae)**

L. umbrosa has been described from SE Sulawesi



(Roos 1997) and so far as I know it is unique for that part of the island. According to my observations, *L. umbrosa* is a very local insect and only rarely encountered within its habitats. Usually, only single specimens can be observed during a day in the field in contrast to *Lohora transiens* Fruhstorfer, 1908 which is very common in the same forest habitats with *Selaginella* spec. as undergrowth. Presumably *Selaginellas* represent the foodplants of the *Lohora* caterpillars as has been shown to be the case for other Satyrinae of the genera *Ragadia*, *Acrophthalmia* and *Euptychia* (Singer et al. 1971; Fukuda 1983; DeVries 1986; Miller & Miller 1988). Apart from the type-locality Sambeani, *L. umbrosa* is also known from Porabua, located northwest of Sambeani (Roos, March 2011), and has also been found recently at the eastern side of Sulawesi Tenggara in the vicinity of Kendari (Roos, March 2015).

L. umbrosa constitutes the SE Sulawesi representative of the subgenus *Physcon* which mostly includes species with dark brown wing colours. *Lohora decipiens* Martin, 1929 is probably closely allied to *L. umbrosa* as substantiated by wing colour pattern and the structure of the male genitalia (not shown) but clearly, the upperside and underside wing colours of *L. umbrosa* are much darker than those of *L. decipiens* (Plate 87 figs 5-8) (Roos 1997). The hindwings of *L. umbrosa* are nearly uniformly dark brown. Obviously, *L. umbrosa* constitutes the species with the darkest wing pattern within the genus. It is assumed that *L. decipiens* and *L. umbrosa* represent sister-species (under investigation) inhabiting clearly separated areas within Sulawesi, i.e. North / Central Sulawesi and SE Sulawesi, respectively.

***Polyura attalus* Felder et Felder, 1867 / *Polyura athamas* Staudinger, 1886 (Nymphalidae)**

Green-coloured species of the *athamas*-group of the genus *Polyura* Billberg, 1820 are obviously rare in Sulawesi. Until recently, only a few specimens of *Polyura alphius* Staudinger, 1886 were known from Sulawesi Selatan. Vane-Wright & de Jong (2003) assume that on Sulawesi the species is restricted exclusively to the South. Surprisingly, a population of a green-coloured *Polyura* was discovered recently in SE Sulawesi. It was found in the vicinity of Porabua in March 2009 and its occurrence in the area was subsequently confirmed as follows: Porabua (March 2011), Konawendepiha (March 2011 and 2015), Andamau (March 2015). Interestingly, however, the specimens do not belong to *P. alphius* but to a different species. From neighbouring islands such

as Borneo, Java and Sumatra, *Polyura athamas* is known (D'Abrera 1984; Otsuka 1988). According to the recent revision of the *athamas*-group by Toussaint et al. (2016), however, who also used DNA sequence data for phylogenetic analyses, the species *P. athamas* occurs in mainland South-east Asia only while it is replaced on the Indonesian islands by *P. attalus* which was given species status by the authors. So, the *Polyura* populations from SE Sulawesi will be tentatively assigned here to *P. attalus* as their belonging to *P. athamas* is less probable. A detailed analysis will clarify its taxonomic assignment (Roos, in preparation). A representative specimen is shown on plate 86 figs 9-10. Albeit, the presence of a 'non-*alphius*' *Polyura* in Sulawesi Tenggara in addition to *P. alphius* is zoogeographically highly interesting because it creates an unusual distribution pattern for this *Polyura*, i.e. a discontinuous area interrupted from west to east by *P. alphius* in Southwest-Sulawesi.

***Parthenos sylvia ornatrix* Tsukada, 1991 (Nymphalidae)**

This is a further peculiarity of SE Sulawesi as subspecies *ornatrix* is exclusively found in that province and as the other parts of Sulawesi are inhabited by an additional unique subspecies of *Parthenos sylvia* Cramer, 1776, namely ssp. *salentia* Hopffer, 1874 (Roos 2012). The differences between the two subspecies in wing coloration but in particular in wing shape raise the question that they may represent two different species. The contact zones or eventually overlapping areas of the two subspecies are not known so far but can be assumed in the northern parts of Sulawesi Tenggara. Their discovery may help to answer these open questions. As *P. sylvia ornatrix* also occurs on Buton Island, this taxon is a good example for the zoogeographically specific connection between mainland SE Sulawesi and its southern offshore islands. Further examples for this distribution type will be discussed below.

***Cirrochroa recondita* Roos, 1996 (Nymphalidae)**

SE Sulawesi bears an endemic species of the genus *Cirrochroa*, *C. recondita*, which is similar to *Cirrochroa eremita* Tsukada, 1985, as already described by Roos (1996). Since its description in 1996 more material has been examined confirming its specificity. This concerns in particular the male wing span which is the smallest within the Sulawesian *Cirrochroa* species. Besides that, *C. recondita* exhibits the darkest coloured wing pattern among the allied *Cirrochroa* from Sulawesi,



such as *C. thule* Felder et Felder, 1860 and *C. eremita*. This property of *C. recondita* has not been analysed in detail but leads over to the next section in which the general trend in wing pattern darkening in butterflies from SE Sulawesi will be highlighted. The northern distribution limits of *C. recondita* have yet to be defined. My own investigations in the eastern parts of Sulawesi Tengah did not reveal the presence of *C. recondita*; instead *C. thule* was found locally common there.

The dark coloration trend in wing patterns

Within the large and intricately structured island of Sulawesi many butterfly species exhibit geographical variation which gave reason to description of subspecies. Definitely, the study of this regional variation will allow conclusions on zoogeographical and evolutionary aspects. Little, however, is known on distinctive colour pattern characters of the butterfly populations from SE Sulawesi compared to those of the other parts of the island. Inspection of material of numerous species revealed that there appears to be a trend for darker wing coloration in butterfly specimens/populations from SE Sulawesi. In some cases, this part of the island harbours even the most 'melanotic forms' within the Sulawesi region as it is defined by Vane-Wright & de Jong (2003). Three species showing this coloration trend have been already discussed above, *Zethera incerta*, *Lohora umbrosa* and *Cirrochroa recondita*. In the following, the respective species will be analysed in more detail by using quantitative methods for describing wing pattern parameters. The creation of new subspecific names is avoided here, but it is attempted to eventually assign the populations of SE Sulawesi to known subspecies. Clear definition of new subspecies would require more material to be analyzed in particular from regions from which material is insufficient or completely lacking such as East Sulawesi.

The genus *Eurema* Hübner, 1819 (Pieridae)

Sulawesi harbours 7 species of the genus *Eurema* of which two, *Eurema irena* Corbet et Pendlebury, 1932 and *Eurema celebensis* Wallace, 1867, are endemic for the Sulawesi Region (Vane-Wright & de Jong 2003) and altogether five of the species occur in SE Sulawesi. Besides predominantly yellow coloured *Eurema* species such as *E. hecabe* Linnaeus, 1758 and *E. blanda* Boisduval, 1836 there are Sulawesi *Eurema*

species with extended dark wing coloration which is expressed in males as broadened marginal bands and in females by general reduction of yellow wing areas including suffusion of the yellow patches with brown coloured scales. The species of the latter group include *E. alitha* Felder et Felder, 1862, *E. tominia* Vollenhoven, 1865 and the endemic *E. celebensis* Wallace, 1867. Based on material of these already dark coloured species from SE Sulawesi it appears that this region harbours their most melanotic subspecific forms from the island. As will be outlined below, these *Eurema* species provide impressive examples from the family Pieridae of the overall south-east melanotic trend.

Eurema alitha Felder et Felder, 1862

According to the recent literature, *Eurema alitha* appears to occur on Sulawesi only in the south-west as ssp. *lorquini* Felder et Felder, 1865 and as ssp. *zita* Felder et Felder, 1865 in the northern parts of the island, thus excluding eastern and south-eastern Sulawesi, i.e. the provinces Sulawesi Tengah and Sulawesi Tenggara (Yata & Morishita 1985; Vane-Wright & de Jong 2003). Correspondingly, large areas of the island are left blank on the distribution map of Yata & Morishita (1985). Outside Sulawesi, the species is widely distributed in the Indo-Malayan realm from Sumatra in the West to Papua in the East and has also been recorded from the islands surrounding Sulawesi including those assigned to the Sulawesi region based on zoogeographical considerations (Vane-Wright & de Jong 2003). For example, *E. alitha* is known to occur on Peleng Island in the Banggai Archipelago (Nieuwenhuis 1946; Detani 1983; Yata 1995; Vane-Wright & de Jong 2003) which is separated by the sea from Sulawesi Tengah by less than 20 km. So the species should be expected to occur also on the eastern peninsula. Also, its presence in SE Sulawesi is probable as it was found on the islands Buton, Muna and Kabaena for example (Jurriaanse & Lindemans 1920). Furthermore, Martin (1920) mentions at least 1 female from Kendari at the east coast of Sulawesi Tenggara. Thus, the distributional gap within Sulawesi does not appear plausible. My own investigations revealed records of *E. alitha* from both Sulawesi Tenggara (Plate 88 figs 1-2 & 4-5) and eastern Sulawesi Tengah. Here, I will focus on characterizing the populations of SE Sulawesi. There is a high variability among specimens of *E. alitha* from SE Sulawesi with respect to wing size and colour pattern. It is attempted here to define several types of variation and to find explanations for their occurrence. Furthermore it will be shown



that in spite of the variability, populations from SE Sulawesi can be clearly distinguished from those of Southwest Sulawesi.

In fact, morphometric analyses of the wing colour pattern of the populations from Sulawesi Tenggara reveal striking differences compared to specimens of the subspecies *lorquini* Felder et Felder, 1865 from Sulawesi Selatan. Quantification of the yellow coloured area on the forewings of male *E. alitha* shows that this area is significantly smaller ($P < 0.0001$, Student t-test) in specimens from Sulawesi Tenggara compared to those from Sulawesi Selatan amounting to 30.9 % and 41.6 % of the total forewing area, respectively (Fig. 1, plate 88 figs 1 & 4). As there are enormous differences in wing span and forewing wing area ranging from 95 mm² to 238 mm² among individuals (analysed in detail below), the yellow coloured area is given as percentage of the total forewing area. Figure 2 demonstrates that the normalized patch size is independent of wing size.

On the hindwings, the broad dark brown margin was also analyzed quantitatively and compared between *E. alitha* from Sulawesi Tenggara and Sulawesi Selatan. The band width was measured at various positions, i.e. along the wing veins and along the intervenosa starting from vein rr to vein ax1 on the left hindwing resulting in 15 values. To allow comparison between individuals of different wing span, the values were normalized on the distance between hindwing base and the end of

vein m1 at the margin. The result in Figure 3 shows that the brown margin is broader over its entire length in specimens from Sulawesi Tenggara ($n = 7$) compared to those from Sulawesi Selatan ($n = 5$). All differences are very significant with P-values between < 0.001 and 0.008 according to Student t-test. In the mean, the margin is 1.4 times broader in specimens from Sulawesi Tenggara (Fig. 4). In summary, the quantitative analyses show that the yellow coloured areas on the forewings and the hindwings of male *E. alitha* are much smaller in specimens from Southeast compared to Southwest-Sulawesi. These differences are independent of butterfly size.

Besides the extended dark coloration, there is another phenomenon particularly observed in *Eurema alitha* which will be analyzed here in more detail. This concerns the broad variation in wing span which has been mentioned before already by Martin (1920). Altogether, 31 specimens from Sulawesi Tenggara (Tra) were analyzed showing a range in wing span from 28.8 mm to 46.5 mm. A closer look on the frequency distribution of the data shows that it is trimodal with maxima around 30, 38 and 44 mm (Fig. 5), so that specimens can be assigned to three different size groups which differ significantly from one another as shown by Student's T-test (Fig. 6). For comparison, five specimens each from Sulawesi Selatan (Sel) and from Sulawesi Tengah (Ten) were included in the analysis. The results indicate that discontinuous

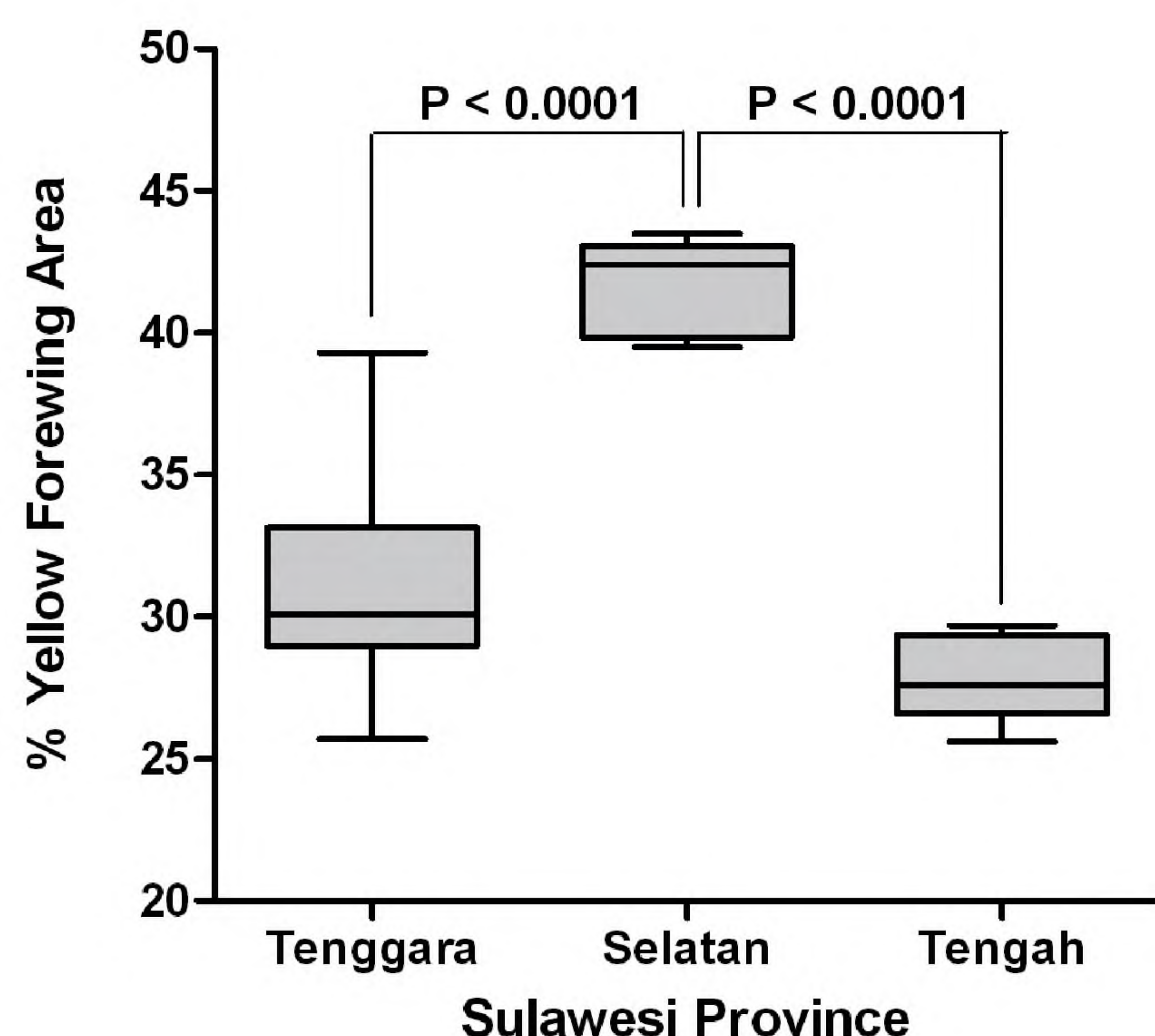


Figure 1. Relative area of the yellow patch on the forewing upperside of *Eurema alitha*. Male specimens from Sulawesi Tenggara ($n = 16$), S.-Selatan ($n = 5$) and Sulawesi Tengah ($n = 5$) were analyzed by FIJI. The patch area was normalized on the total wing area and is given as percentage. Significant differences as indicated (Student's T-test).

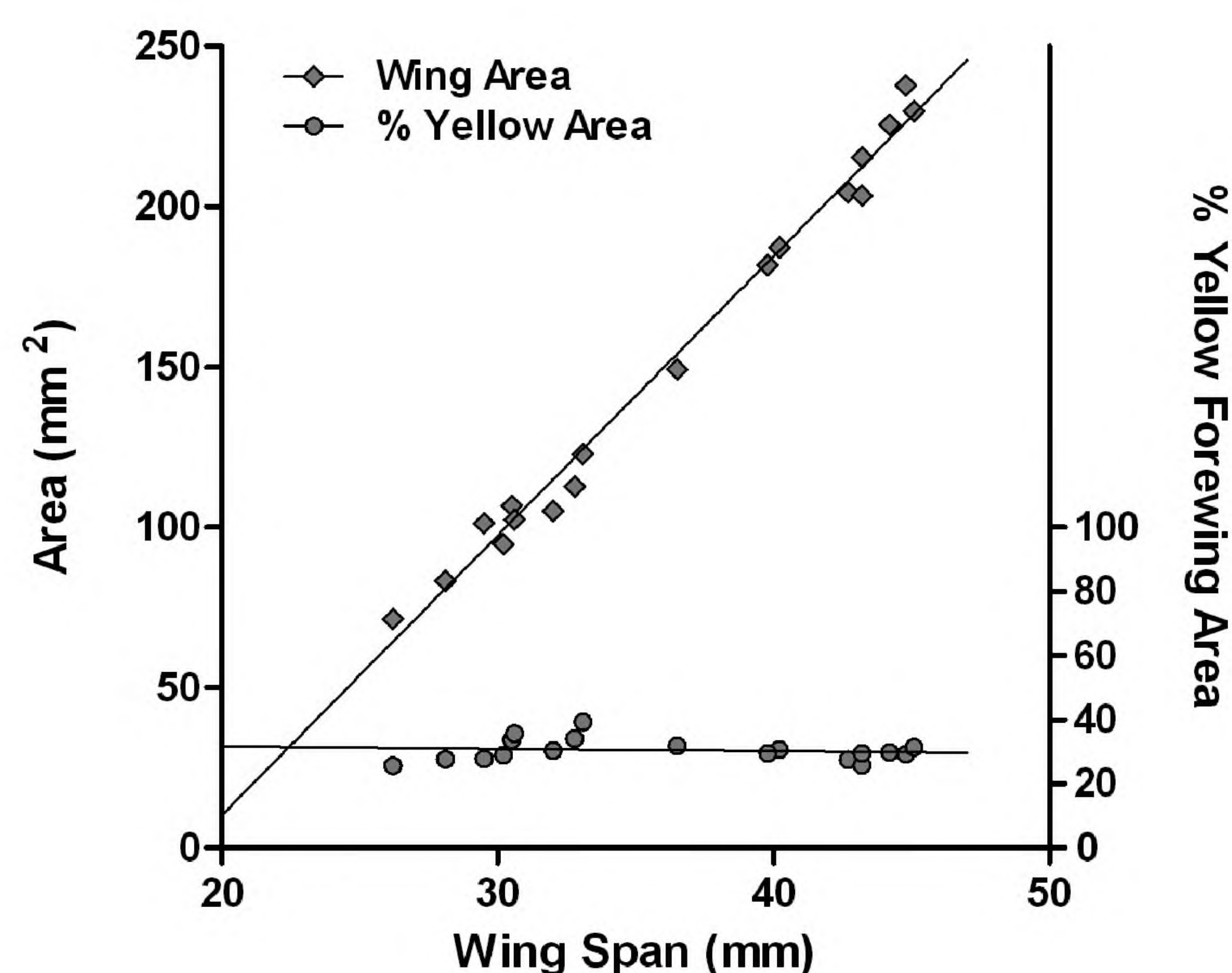


Figure 2. Forewing area and normalized area of the yellow forewing patch of *Eurema alitha* as functions of wing span. For the analysis 18 males were used of which 16 came from Sulawesi-Tenggara. Two further small specimens originate from Koyoan, Luwuk vicinities in Sulawesi Tengah. While there is a linear correlation between wing span and wing area the % yellow area is independent of wing span and thus also of wing area.



size distribution also occurs in *E. alitha* populations of other areas in Sulawesi, at least in Sulawesi Tengah.

The question arises which processes underlie this characteristic frequency pattern in size. Availability or quality of larval food, which may vary seasonally, does not well explain the findings as a more continuous data distribution should be expected. Instead, however, distinct size groups are observed each with its own internal variability.

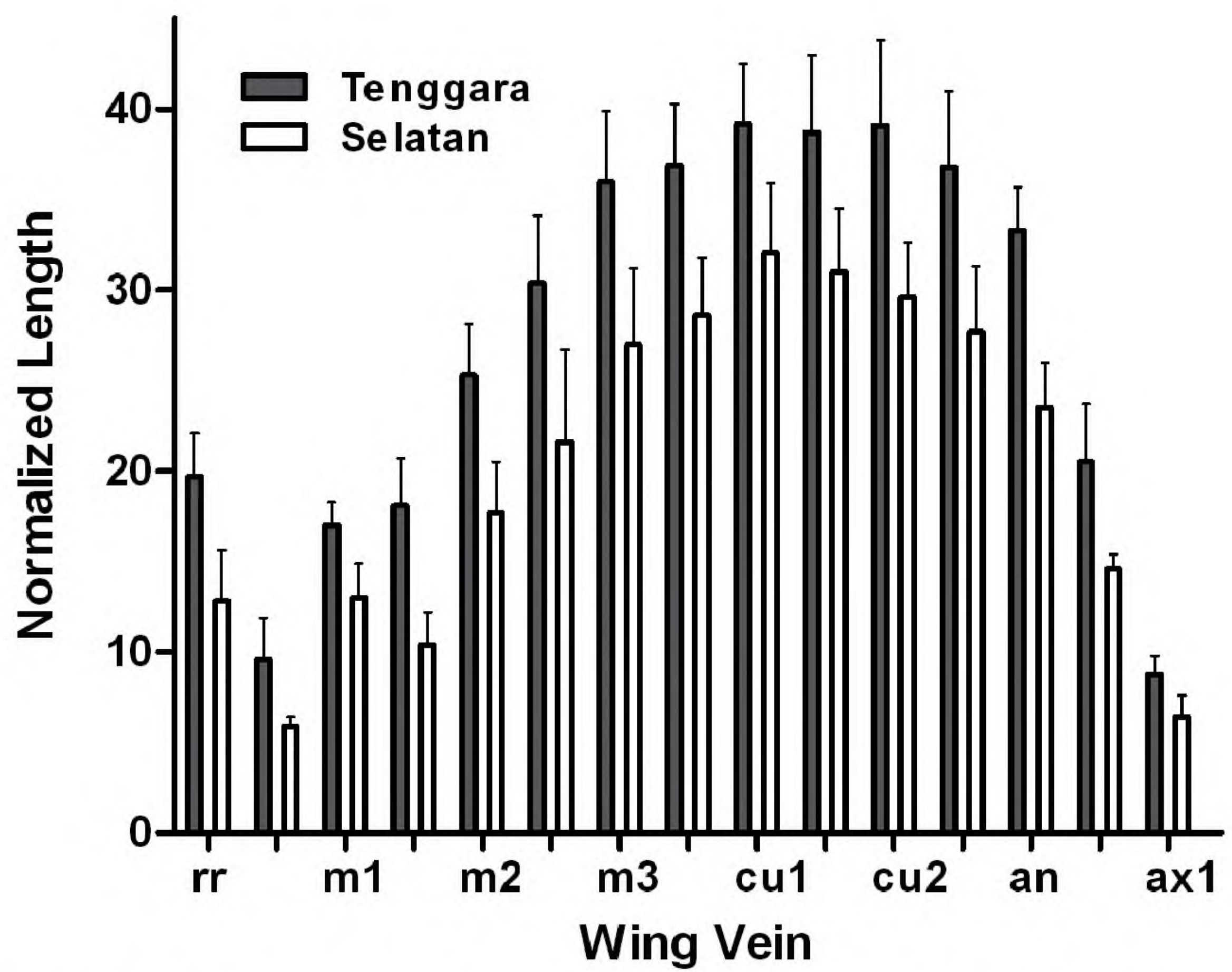


Figure 3. Width of the brown margin of the hindwing upperside in *Eurema alitha* specimens from Sulawesi Tenggara (n = 7) and Sulawesi Selatan (n = 5). Data pairs for the width at the indicated wing vein are followed each by the data of the subsequent intervenosa. To account for butterfly size differences, the values were normalized on the distance between wing basis and end of vein m1. For the significance of differences see text.

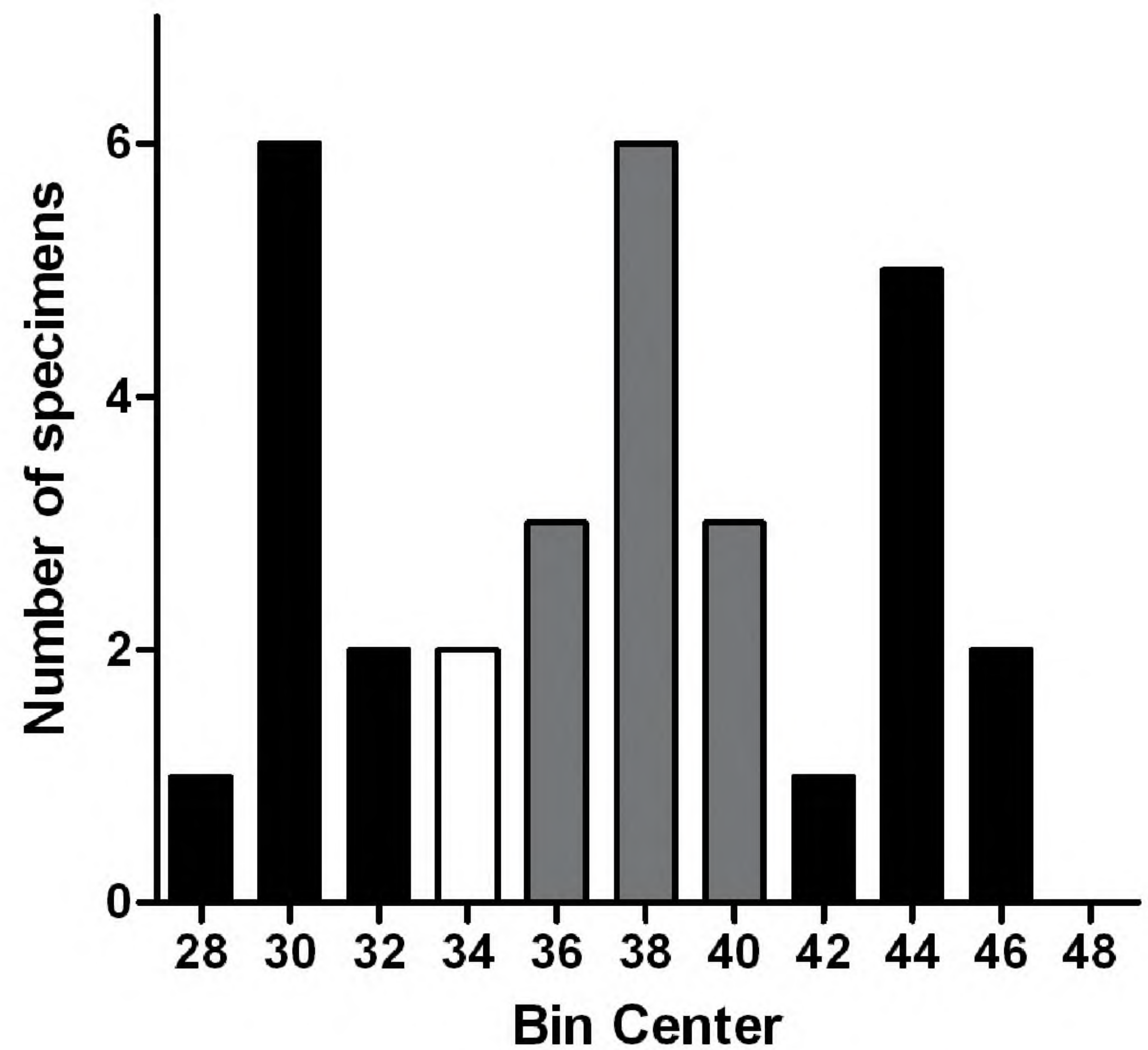


Figure 5. Trimodal size distribution of wing span in *Eurema alitha* from Sulawesi Tenggara. Altogether 31 specimens were used for the analysis. GraphPad Prism was used for calculating the frequency distribution and its presentation vertical scatter plot.

Assuming different numbers of larval stages necessary until final pupation appears to be a plausible hypothesis. The usual number of instars for *Eurema* species is five, as has been shown for *E. laeta* Boisduval, 1836, *E. hecabe* Linnaeus, 1758 and *E. desjardinsii* Boisduval, 1833 (Bogtapa et al. 2015; Clark & Dickson 1965; Sharma 2006). There is only little information on the variability of instar numbers in *Eurema* species. Ooi (1992) observed that dependent on the food plant an additional

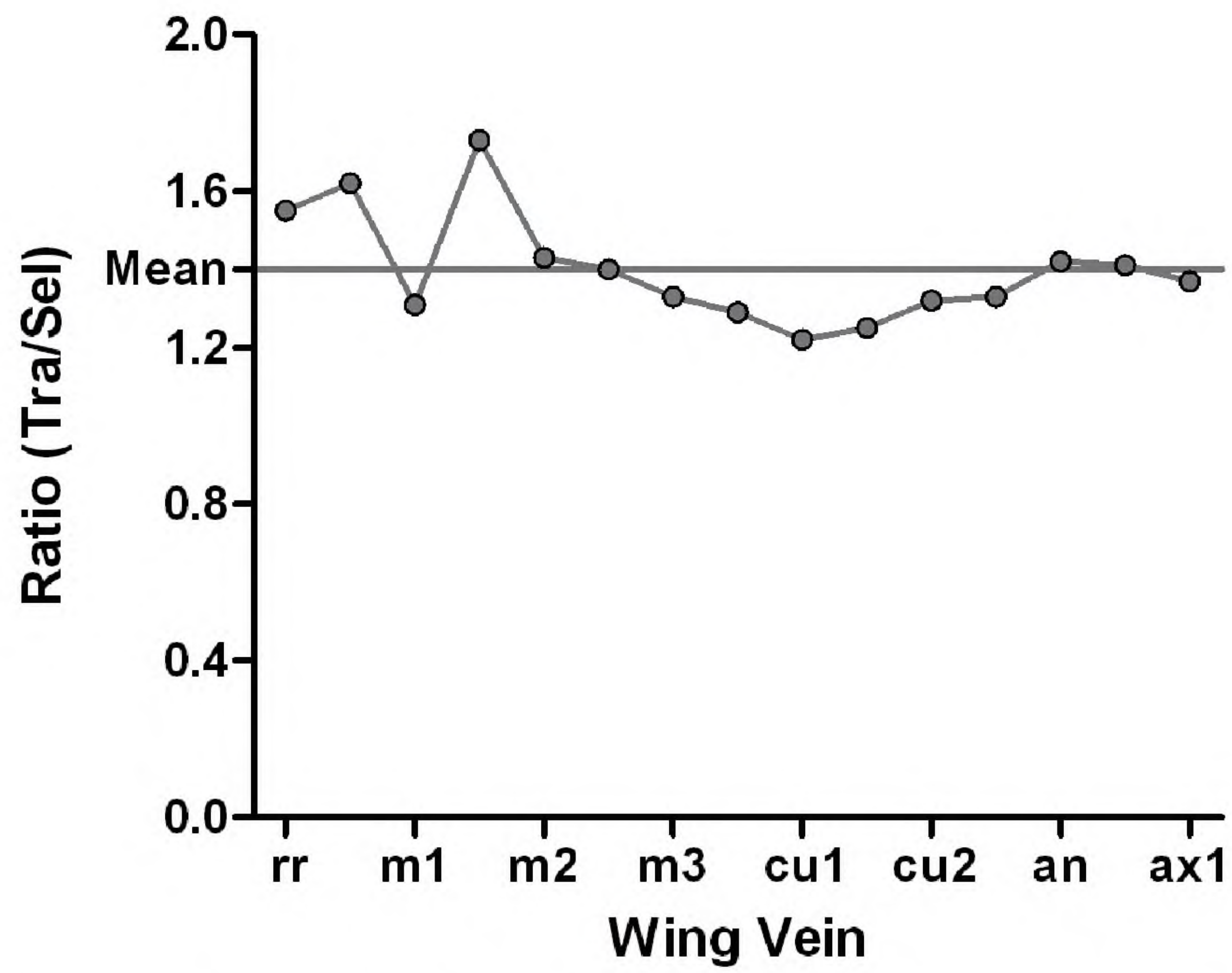


Figure 4. Width of the brown hindwing margin at the different wing veins and the intervenosa of *Eurema alitha* given as the ratio between specimens from Sulawesi Tenggara (Tra, n = 7) and Sulawesi Selatan (Sel, n = 5). Left hindwings were used for the analysis. The mean value of all ratios is 1.40 as indicated by the line).

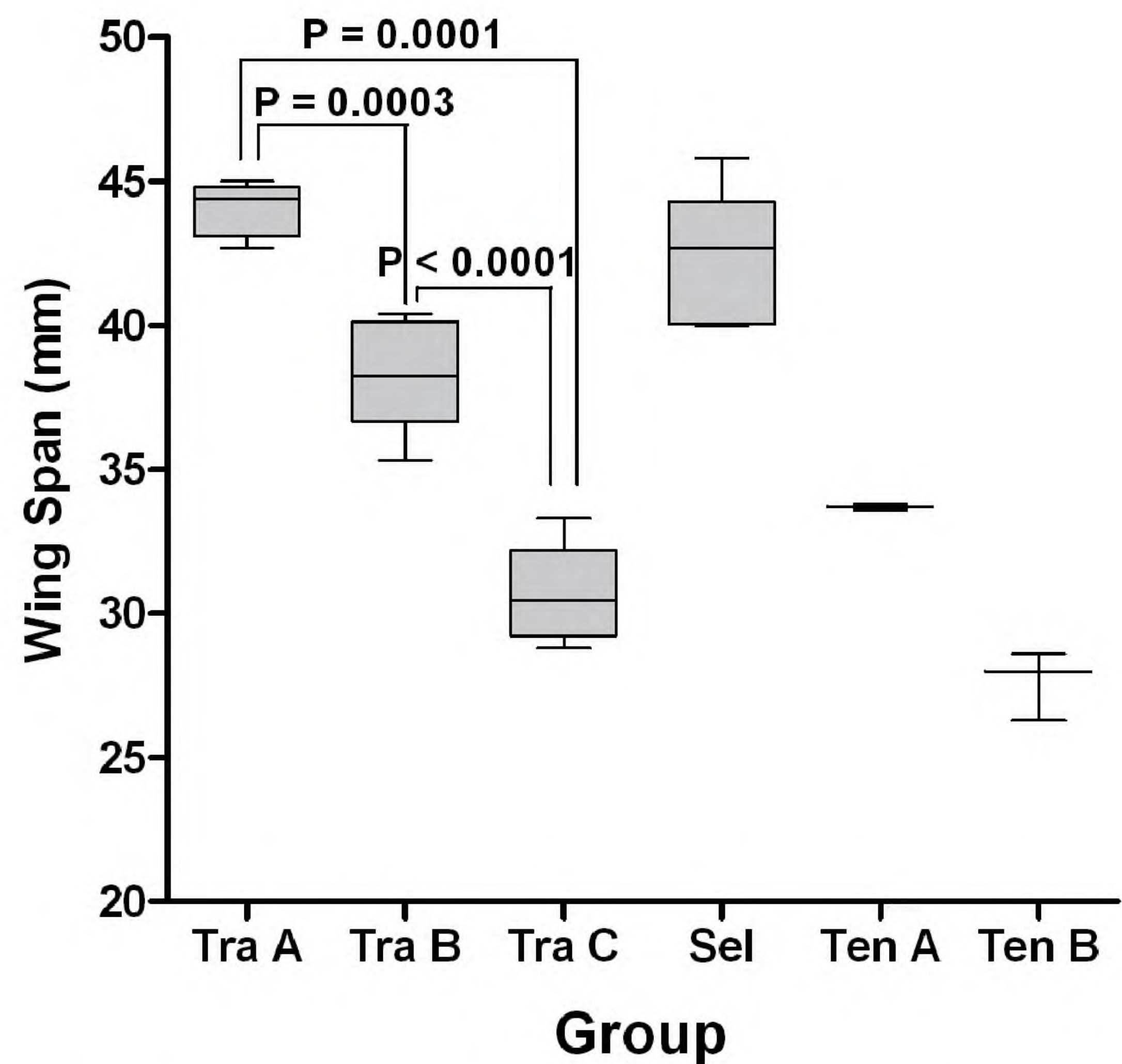


Figure 6. Box plot of wing sizes calculated from specimens of the 3 different size classes of *Eurema alitha* from Sulawesi Tenggara (Tra A, n = 7; Tra B, n = 8; Tra C, n = 10). For comparison, plots are also shown for specimens from Sulawesi Selatan (Sel, n = 5) and from Sulawesi Tengah (Ten A, n = 2; Ten B, n = 3). The differences between the size classes are statistically significant as indicated.



sixth instar can occur in *Eurema hecabe*. However, the length of the larvae and also the head capsule width of the final 5th or 6th instar were identical so that size of the imagines can also be expected to be the same, irrespective of the development via 5 or 6 instars. This latter phenomenon was also recorded for some Satyrinae species (Roos, in preparation). Under the assumption that the middle sized specimens of *E. alitha* develop via 5 instars and the smaller and larger ones by 4 and 6, respectively, the function shown in Figure 7 is obtained by linear regression. It is noted that the line crosses the y-axis close to zero thereby giving a further support for the ‘larval instar’ hypothesis. For this, quite different underlying regulatory mechanisms must be responsible in contrast to the food plant dependent development of *E. hecabe* described by Ooi (1992).

Differences in wing size and in the extent of dark coloured wing areas of butterflies are often associated with seasonal variation, i.e. dry and wet season forms. This phenomenon has also been shown for *Eurema*-species (Jones 1992; Daniels 1995). The results presented above are obtained exclusively from wet season specimens from both Southwest and SE Sulawesi. Based on only six males from Sulawesi Tenggara taken in the dry season in October, it is shown that there are also season-dependent differences in the wing pattern areas (Fig. 8) while the wing span does not appear to be affected (Fig. 9). Similar to the wet season form, the relative area of the yellow patch is independent of the wing size. The calculated slope for the function % yellow forewing area vs. absolute forewing area statistically does not differ from zero

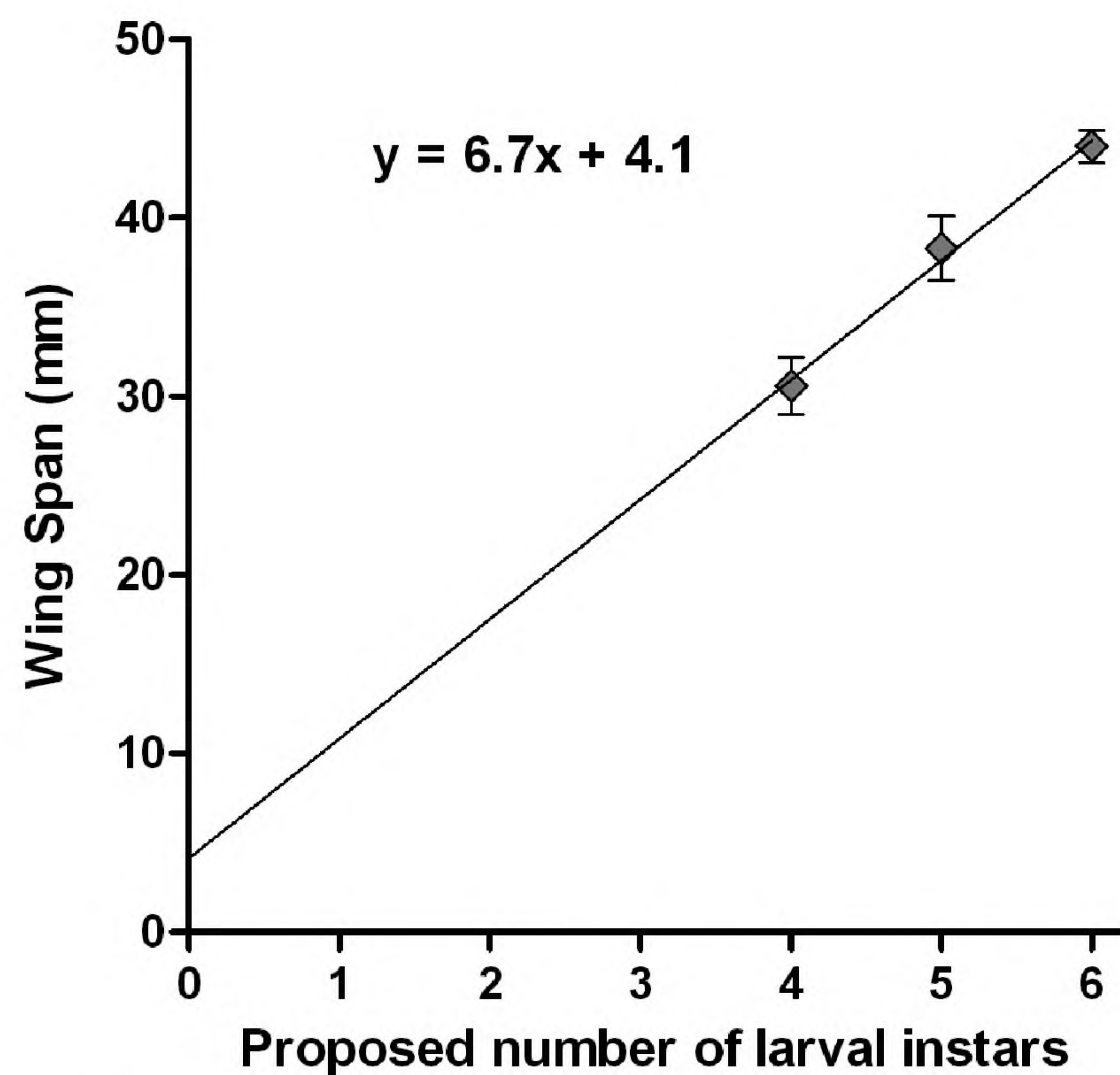


Figure 7. Presentation of the wing span of male *Eurema alitha* butterflies as a hypothetical function of the proposed number of larval instars (see text).

(Fig. 10). Daniels (1995) compared forewing lengths of dry and wet season forms of 3 different *Eurema* species from Florida, U.S.A. Significant differences were recorded but they were less pronounced than between the season-independent size classes of *E. alitha* described here. Jones (1992) showed that forewing length as well as the colour pattern, i.e. the portion of dark versus yellow areas, seasonally varies among six Australian *Eurema* species. In summary, there appear several mechanisms causing variability in wing size, in colour pattern and in the development of *Eurema* species:

1. *Eurema alitha* from different populations: Region dependent variation in the extent of dark pattern elements. The yellow patch is significantly reduced in specimens from Sulawesi Tenggara compared to those from Sulawesi Selatan (Fig. 1).
2. *Eurema alitha* from Sulawesi Tenggara: Seasonally dependent alteration of the yellow wing area with smaller areas in the wet season form (Fig. 8).
3. *Eurema alitha* from Sulawesi Tenggara: Seasonally independent substantial variability in wing size with a trimodal frequency distribution (Fig. 9) not influencing the extent of colour pattern.
4. *Eurema* sp. from Australia: Seasonally concomitant variation in size and colour pattern (Jones 1992).
5. *Eurema hecabe* Linnaeus, 1758 from Malaysia:

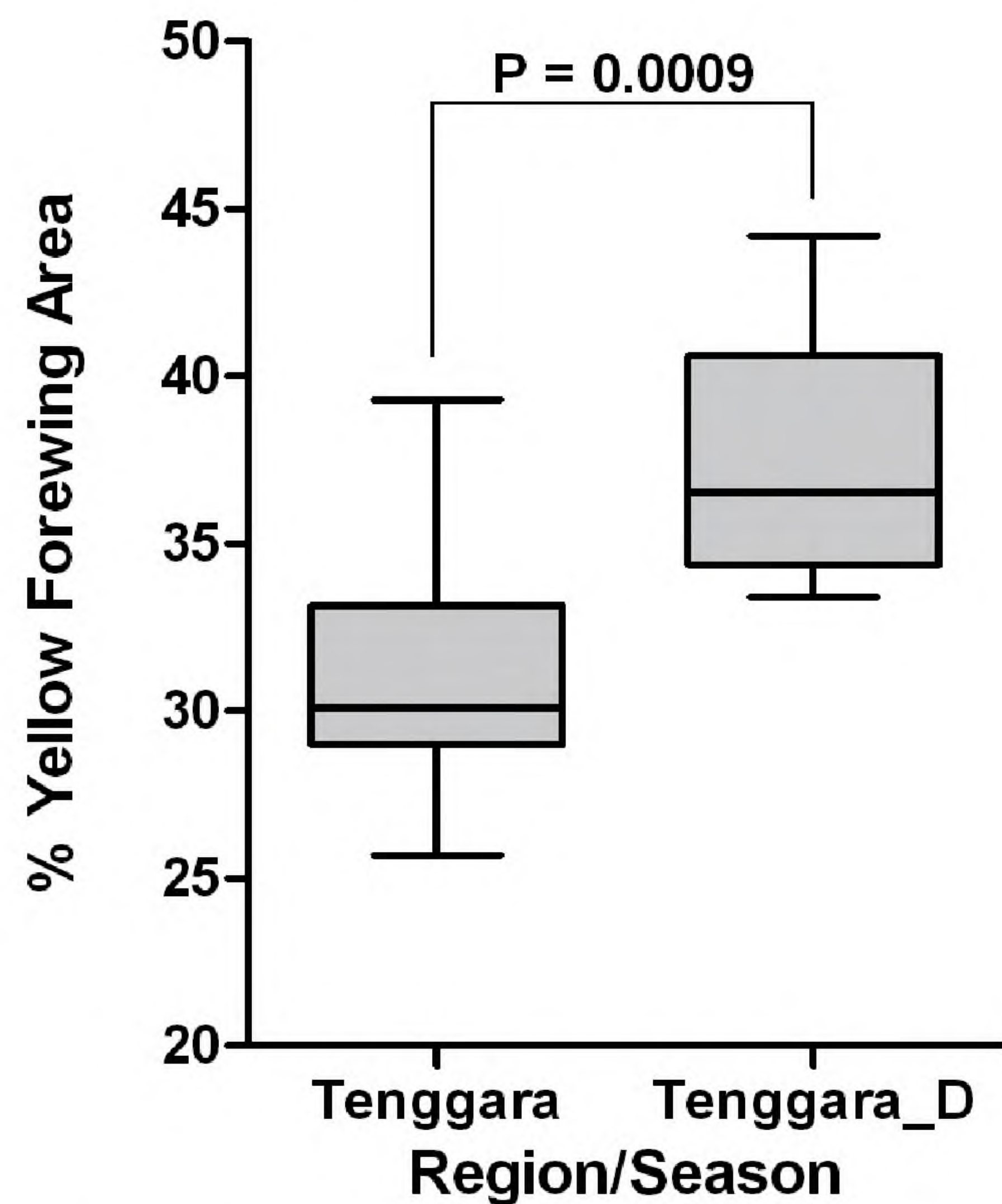


Figure 8. Differences in the size of the yellow forewing area in wet (_W) and dry season (_D) specimens of *Eurema alitha* from Sulawesi Tenggara. The relative size of the yellow patch normalized on the total forewing area is plotted. Number of specimens analyzed: Tenggara_W, n = 16, Tenggara_D, n = 6. In spite of the overlap between values of the two samples the difference is statistically significant.



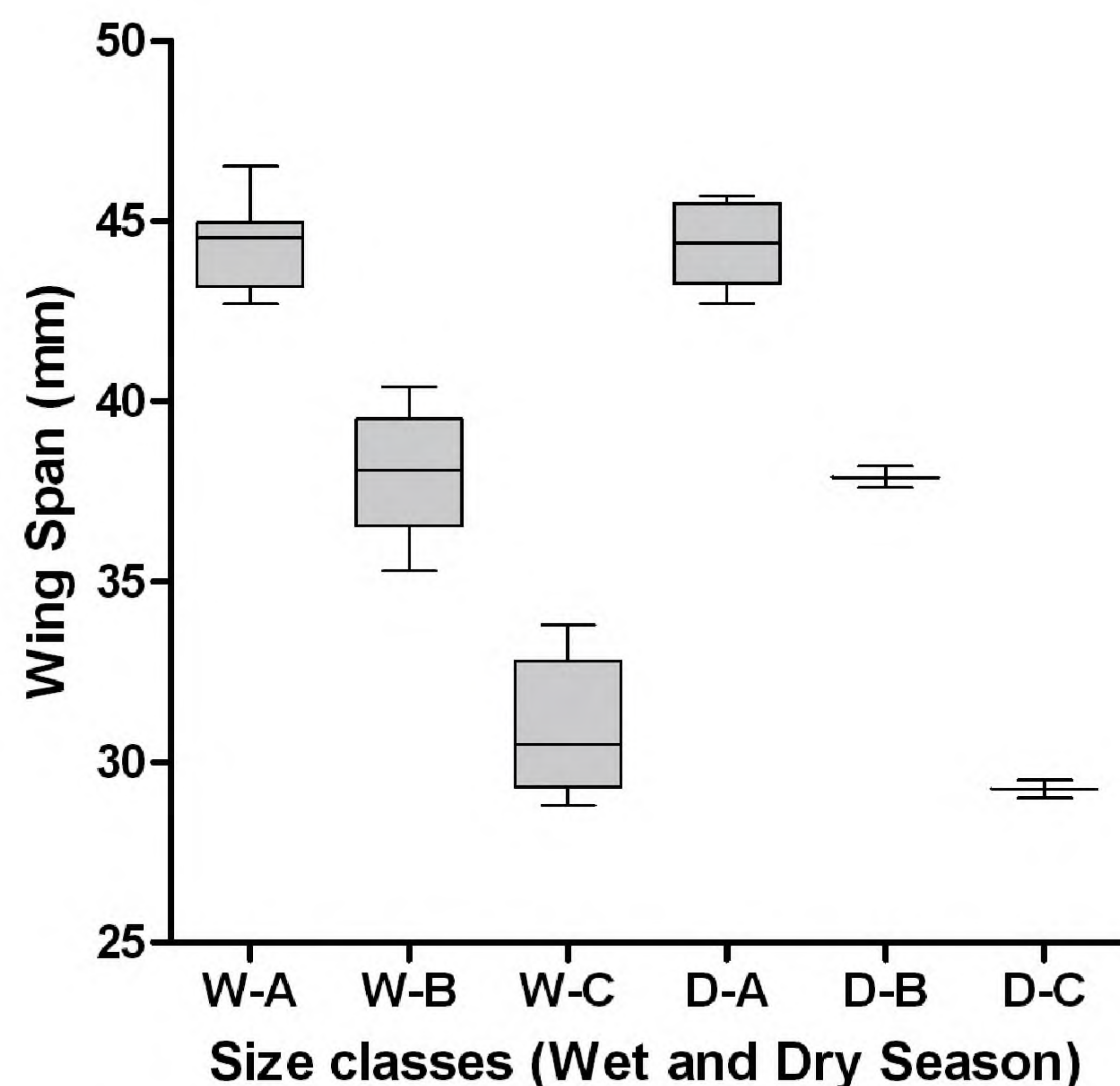


Figure 9. Wing span (mm) of *Eurema alitha* from the wet (W) and dry season (D) in Sulawesi Tenggara. Box-plots for the three identified size classes A – C are shown. Number of analyzed individuals: W-A, n = 8; W-B, n = 12; W-C, n = 11; D-A, n = 5; D-B, n = 2; D-C, n = 2.

Food plant dependent development via five or six instar larvae (Ooi 1992).

In females of *E. alitha*, the trend to more melanotic phenotypes in SE Sulawesi is even more pronounced (Plate 88 fig. 2) than in males. However, a quantitative analysis has not yet been performed. Judged from the wing coloration, *E. alitha* from Sulawesi Tenggara resembles much more the northern ssp. *zita* Felder et Felder, 1865 than ssp. *lorquini* Felder et Felder, 1865. Vane-Wright & de Jong (2003) also include populations of Banggai in ssp. *zita* but leave open the subspecific assignment of populations of the islands south of Sulawesi Tenggara. Both, Jurriaanse & Lindemans (1920) and Martin (1920) list the latter under the name *zita*, Martin (1920) even in the rank of a species. In a preliminary study with limited material of *E. alitha* from Muna Island it can be shown here that the colour pattern resembles that of the populations from SE Sulawesi (Fig. 11). In addition, this is also true for populations of Sulawesi Tengah (Fig. 11). A detailed morphometric comparison with ssp. *zita* from North Sulawesi has not yet been performed. Based on figures in Yata (1995), the yellow area on the forewing of a male from Manado [= Manado] in North Sulawesi is of similar size as in specimens from Sulawesi Tenggara, i.e. 32.2% of the forewing area vs. a mean of 30.9%, respectively.

***Eurema tominia* Vollenhoven, 1865**

In addition to the Sulawesi region, *E. tominia*

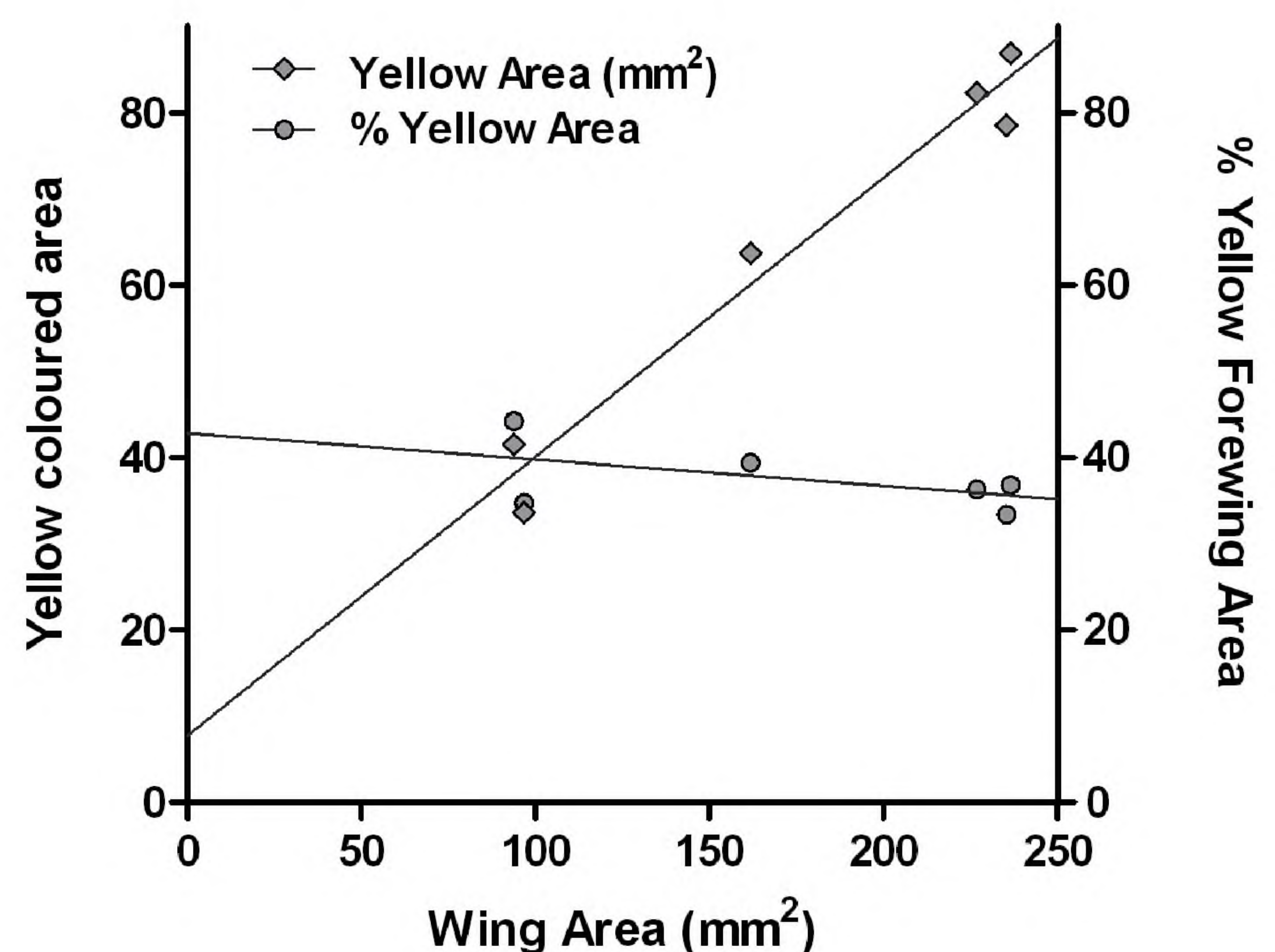


Figure 10. Extent of the yellow coloured forewing area of the dry season form of male *Eurema alitha* from SESulawesi as a function of the total forewing area. For the yellow area absolute values (Raute) and relative values (circles) were used. The latter were calculated by normalization of the absolute values on the total forewing area. While a nearly linear correlation is obtained between the absolute values the normalized patch area is independent of wing size (statistically, the slightly negative slope does not derive from zero).

occurs in Borneo. From Sulawesi Island only one subspecies is known, the nominate ssp. *tominia* (Corbet & Pendlebury 1932; Yata & Morishita 1985; Otsuka 1988) while a number of subspecies from adjacent islands are recognized (Vane-Wright & de Jong 2003). The various *E. tominia*-subspecies described from Sulawesi, particularly by Fruhstorfer, such as *toradja* Fruhstorfer, 1910, *zamida* Fruhstorfer, 1908 and *tondana* Felder, 1875 were not mentioned by Martin (1920) except for *battana* Fruhstorfer, 1908, which he considers to be the subspecies from South Sulawesi. Later, all of these subspecies were synonymized by Corbet & Pendlebury (1932) and also not accepted by most subsequent authors (Yata & Morishita 1985; Vane-Wright & de Jong 2003). As an exception, only D'Abrera (1982) lists 3 subspecies from Sulawesi, the nominate subspecies *tominia* for North Sulawesi, ssp. *battana* for South Sulawesi and ssp. *toradja* for East Sulawesi. There are no literature data on the occurrence of *E. tominia* in SE Sulawesi. Also Jurriaanse & Lindemans (1920) do not list *E. tominia* in their publication on butterflies from SE Sulawesi. My own investigations, however, prove its presence from several localities in SE Sulawesi and show that these populations differ by their wing markings from those occurring in other parts of the island. The following locations and data



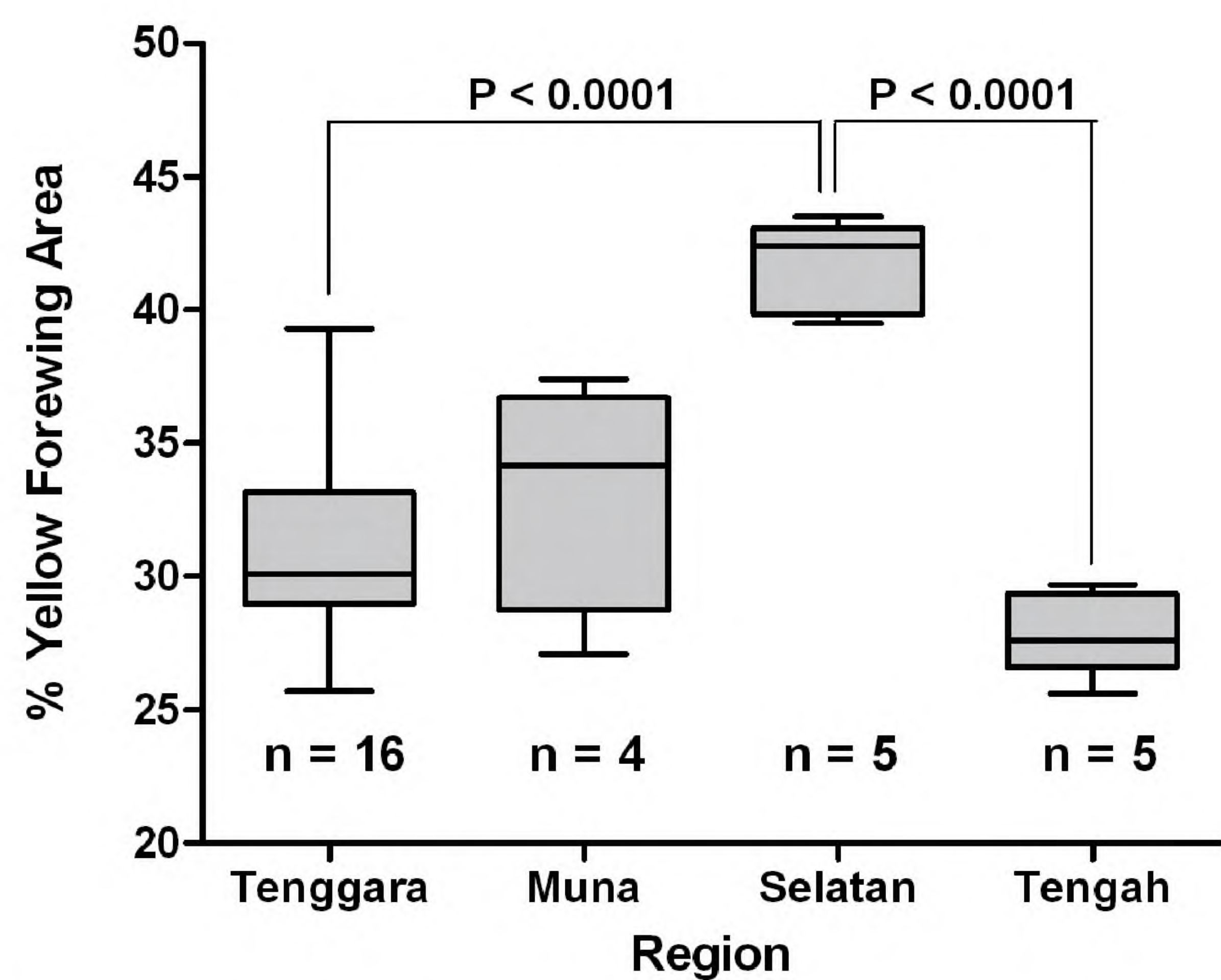


Figure 11. Relative extent of the yellow forewing area between *Eurema alitha* from various regions of Sulawesi (Tenggara, Selatan, Tengah) and Muna Island. Number of analyzed individuals (n) and statistical significance (P) as indicated.

can be listed for *E. tominia*:

Andamao	15.III.2013
Kolaka	22.X.2005, 29/30.III.2009, 01.IV.2009, 17/19/21.III.2011
Porabua	18.III.2013, 16.III.2015
Sambeani	28.II.1999, 02.III.1999

As in *E. alitha*, the south-eastern *E. tominia*-subspecies is characterized by reduced yellow-coloured areas on the wings' upperside compared to nominotypical *E. tominia* from Sulawesi Selatan (Fig. 12, plate 88 figs 7-10). In the mean (M), the portion of the yellow area on the forewing uppersides amounts to 36.8% compared to 20.7% in specimens from Sulawesi Selatan and Sulawesi Tenggara, respectively. Figure 12 shows the data for individual specimens (numbers) and the corresponding mean values including standard deviations (M). There is only little variation in the normalized values for the size of the yellow patch although there are substantial differences in the total forewing area in *E. tominia* individuals from SE Sulawesi. Due to insufficient material it cannot be concluded whether there are discrete size classes in *E. tominia* similar to *E. alitha*.

Female specimens from SE Sulawesi have nearly completely dark brown forewings, i.e. the yellow pattern elements are completely or largely missing (Plate 88 figs 3 & 6). In this respect they resemble *E. celebensis* ssp. *exophthalma* Fruhstorfer (see below) from Sula Island and represent the darkest form of mainland Sulawesi. Further material of female *E. tominia* is needed for a more comprehensive analysis.

***Eurema celebensis* Wallace, 1867**

Typical *E. celebensis* was described from Makassar in Southwest Sulawesi (Wallace 1867). A further subspecies, ssp. *exophthalma* Fruhstorfer, 1910, which is characterized in males by broad dark forewing margins and in females by nearly completely dark brown coloured wings, occurs on the Sula Islands and in the Banggai Archipelago, located in the East of the Sulawesi region. Corbet & Pendlebury (1932) state that "As a rule specimens from South Celebes are slightly larger and more yellow than those from North Celebes". This is not true, however, for the populations from SE Sulawesi which may be assigned to ssp. *exophthalma*. Females from Sambeani and Porabua (Sulawesi Tenggara) are completely or nearly devoid of yellow markings on their forewings and males from that region show broader brown forewing margins compared to specimens from the southwest (Plate 89 figs 1-11). So, we can extend the distribution area of ssp. *exophthalma* from the Sula- and Banggai-Islands (Detani 1983; Yata 1991) to SE Sulawesi. Accordingly, the distribution map in Yata & Morishita (1985) has to be revised. There is little information on *E. celebensis* and the occurring subspecies from Central and East Sulawesi. It is noted that a female *E. celebensis* taken near Koyoan in Sulawesi Tengah shows nearly complete dark brown forewings (Air Terjun Dendengan, Koyoan, west of Luwuk, Sulawesi Tengah, March 2015, P. Roos) (Plate 89 fig. 12). It is assumed that the area of ssp. *exophthalma* also includes East Sulawesi.

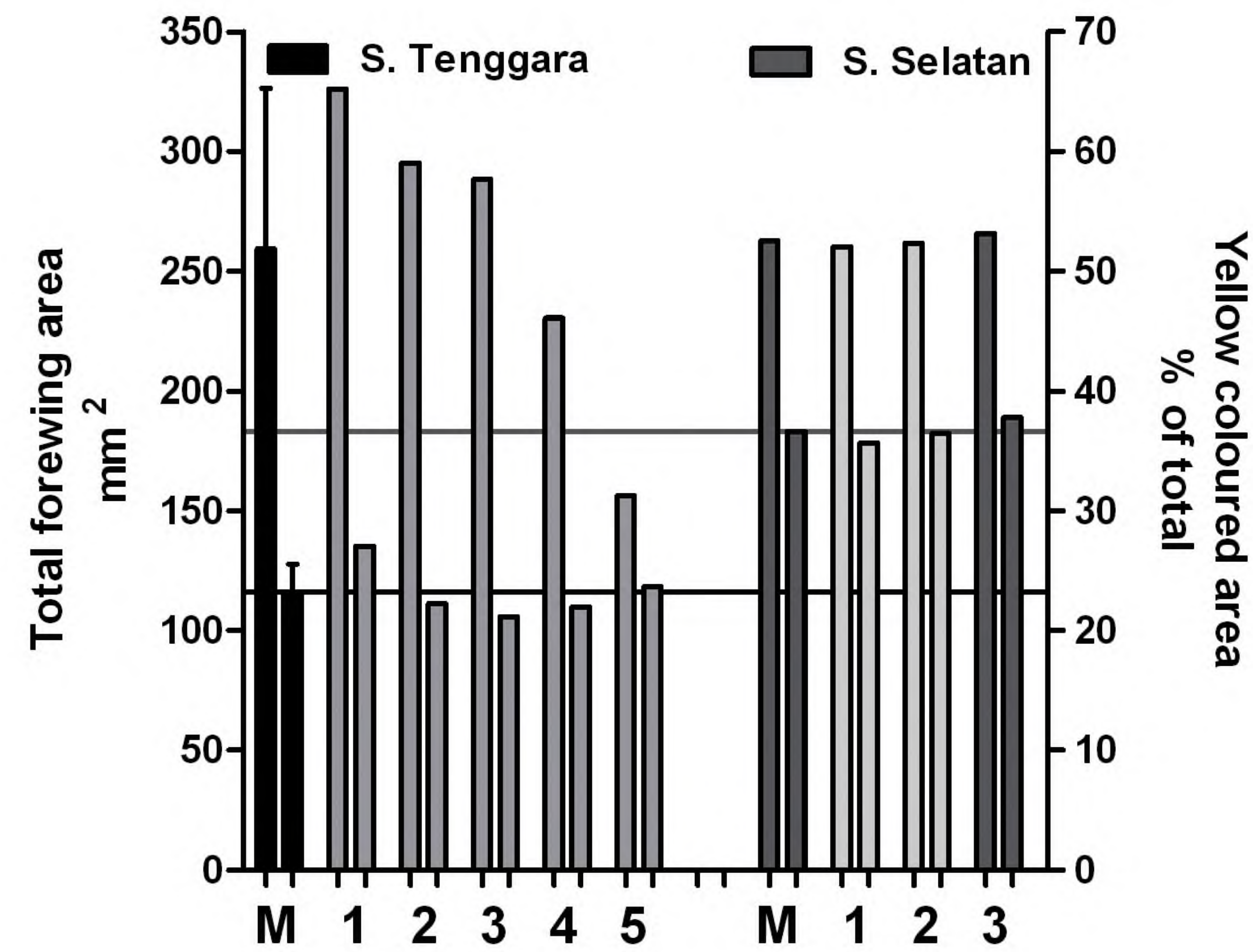


Figure 12. Total forewing area and relative extent of the yellow coloured forewing area of *E. tominia* from Sulawesi Tenggara and Sulawesi Selatan. Left and right bar of each pair represent the total forewing area and the yellow coloured area in % (right ordinate), respectively. Mean values (M) and data for individual specimens (n = 5 and n = 3) are shown. The means of the yellow patch sizes of the two different populations are each indicated by a line.



As stated by several authors (Martin 1920; Yata & Morishita 1985; Yata 1991) and based on own observations *E. celebensis* is rather rare and does not form dense populations as is known for other *Eurema* species (Roos 2000). Three males of *E. celebensis* from each of Sulawesi Tenggara and Sulawesi Selatan, which are shown in figs 1-3, 7-9 on plate 89, were used for a quantitative analysis of the yellow forewing area. For this the total area and the yellow coloured area

of both forewings were quantified by means of the FIJI software and the mean values calculated. Then the percentage of the yellow area related to the total wing area was determined. Finally, means and standard deviations were calculated including the three specimens of each subspecies. Furthermore, the wing span of each specimen was determined. The data are summarized in the Table 1:

Table 1. Forewing area, wing span and relative extent of the yellow coloured forewing patch of male *E. tominia* Vollenhoven, 1865 from Sulawesi Tenggara and Sulawesi Selatan.

Legends: Wing span is also given for females; s – significant; ns – not significant; number of specimens analyzed in each group as indicated.

	Sulawesi Tenggara (n = 3)	Sulawesi Selatan (n = 3)	Significance Student's T-test
% yellow area	36,5 ± 4,1	48,6 ± 2,3	P = 0.011 s
wing area (mm ²)	105,4 ± 21,5	141,3 ± 19,8	P = 0.100 ns
wing span (mm)			
males	31,1 ± 3,7	36,0 ± 2,8	P = 0.141 ns
females	36,0 ± 1,0	37,8 ± 1,4	P = 0.144 ns

The quantitative analyses reveal a clear and significant (P = 0.011) difference in wing coloration between the two subspecies. The differences in wing span and wing area are not significant. More material is needed for the analyses to prove the obvious differences in wing size which are absolute values in contrast to the quantified yellow patch which is normalized on the wing area. As has been shown above for *E. alitha* different size classes also do exist in *E. celebensis* affecting the statistical analysis in particular of small samples, n = 3 in this case.

Ceporia eperia Boisduval, 1836 (Pieridae)

Martin (1920) states that *C. eperia* is abundant on Sulawesi at higher elevations and rare in coastal areas. Also, Yata & Morishita (1985) give entire Sulawesi as the distribution area for the species, although there are no literature records which document its occurrence in East and SE Sulawesi. Accordingly, Iwasaki & Yata (2005) give North and South Sulawesi as area for *C. eperia* and selectively exclude Central, East and SE Sulawesi. Additionally, the authors list *C. eperia* for the island Buton which is located to the south of SE Sulawesi and describe the ssp. *flava* Iwasaki et Yata, 2005 from there. This subspecies is characterized by the extension of the black forewing markings compared to the nominotypical form. I have found *C. eperia* also on mainland SE Sulawesi. These specimens show broader black

wing markings and are therefore tentatively assigned here to ssp. *flava*. A specimen from SE Sulawesi is shown on plate 88 figs 11-12. I can give the following locations and dates for *C. eperia* in Southeast Sulawesi: Kolaka (March 1994), Porabua (March 2009) and Konawendepiha (March 2011). Based on my observations, the species is much rarer in this region than *Ceporia timnatha* Hewitson, 1862.

The genus Cyrestis Boisduval, 1832 (Nymphalidae: Biblidinae)

According to the current state of knowledge, the genus *Cyrestis* comprises altogether 4 species on Sulawesi Island and a fifth one *C. eximia* Oberthür, 1879 occurs on Sangihe within the Sulawesi Region. Up to now, 3 *Cyrestis* species are known from Sulawesi Tenggara: *C. strigata* Felder et Felder, 1867, *C. paulinus* Felder et Felder, 1860 and *C. thyonneus* Cramer, 1779 while *C. heracles* Staudinger, 1896 is missing. According to Vane-Wright & de Jong (2003), the latter species is restricted to North and Central Sulawesi but Tsukada et al. (1985) marks only the northern peninsula on the distribution map. My own observations, however, have proven the presence of *C. heracles* in the eastern parts of Sulawesi Tengah (Koyoan, vic. Luwuk, Sulawesi Tengah, 07.iii.2015). Jurriaanse & Lindemans (1920) also do not mention *C. heracles* from the Islands Buton and Kabaena. The absence of *C. heracles* from SE Sulawesi and its



presence in East Sulawesi is of zoogeographical interest as there are otherwise many similarities and congruencies between the two areas with respect to the distribution of butterfly species and subspecies. In this case, the non-existence of the species *C. heracles* in the Southeast is a peculiarity (see section below). Corbet and Pendlebury (1992) and Holloway (1973) claim the presence of *Cyrestis cocles* Fabricius, 1787 on Sulawesi; this cannot currently be substantiated.

***Cyrestis strigata* Felder et Felder, 1867**

According to my own observations, *C. strigata* is the most common among the four *Cyrestis* species occurring on Sulawesi and appears to occur all over the island (Martin 1924). However, Jurriaanse & Lindemans (1920) do not mention the species from Sulawesi Tenggara but from the off-shore islands Wowoni and Buton located on the east and south coast of that province. Also, Martin (1903), Martin (1924) and Tsukada et al. (1985) do not list any locality for *C. strigata* in SE as well as in East Sulawesi. My own surveys have shown its presence in Sulawesi Tenggara from the following places: Kolaka, Sambeani, Lasada, Asolu, Porabua and Andamau – all located north of the line between Kolaka and Kendari from the west and east coast. The upperside wing pattern of *C. strigata* is

variable, particularly concerning the extension of the white median band. This pattern element has been analyzed quantitatively in two different ways:

- 1. The width of the band in the forewing cells has been quantified individually and related to the forewing length to account for size differences as mentioned before;
- 2. The area of the band on the forewings has been determined and then related to the total wing area as percentage. The populations from SE Sulawesi statistically differ in the extension of the median band from those occurring in the northern parts of South Sulawesi, i.e. from Sumarorong and Rantepao. The white band is clearly broader in the latter (Figs 13-14; plate 89 figs 13-18).

By both methods mentioned above, concerning total band area as well as the band width in all forewing cells, the differences between specimens from Sulawesi Tenggara and Sulawesi Selatan are statistically significant. A comparison between specimens from further parts of Sulawesi, revealed that the band extension for the populations from SE Sulawesi is nearly identical to those from East Sulawesi and is similar, but significantly broader ($P = 0.026$) in specimens from southern South Sulawesi (Bantimurung) (Fig.

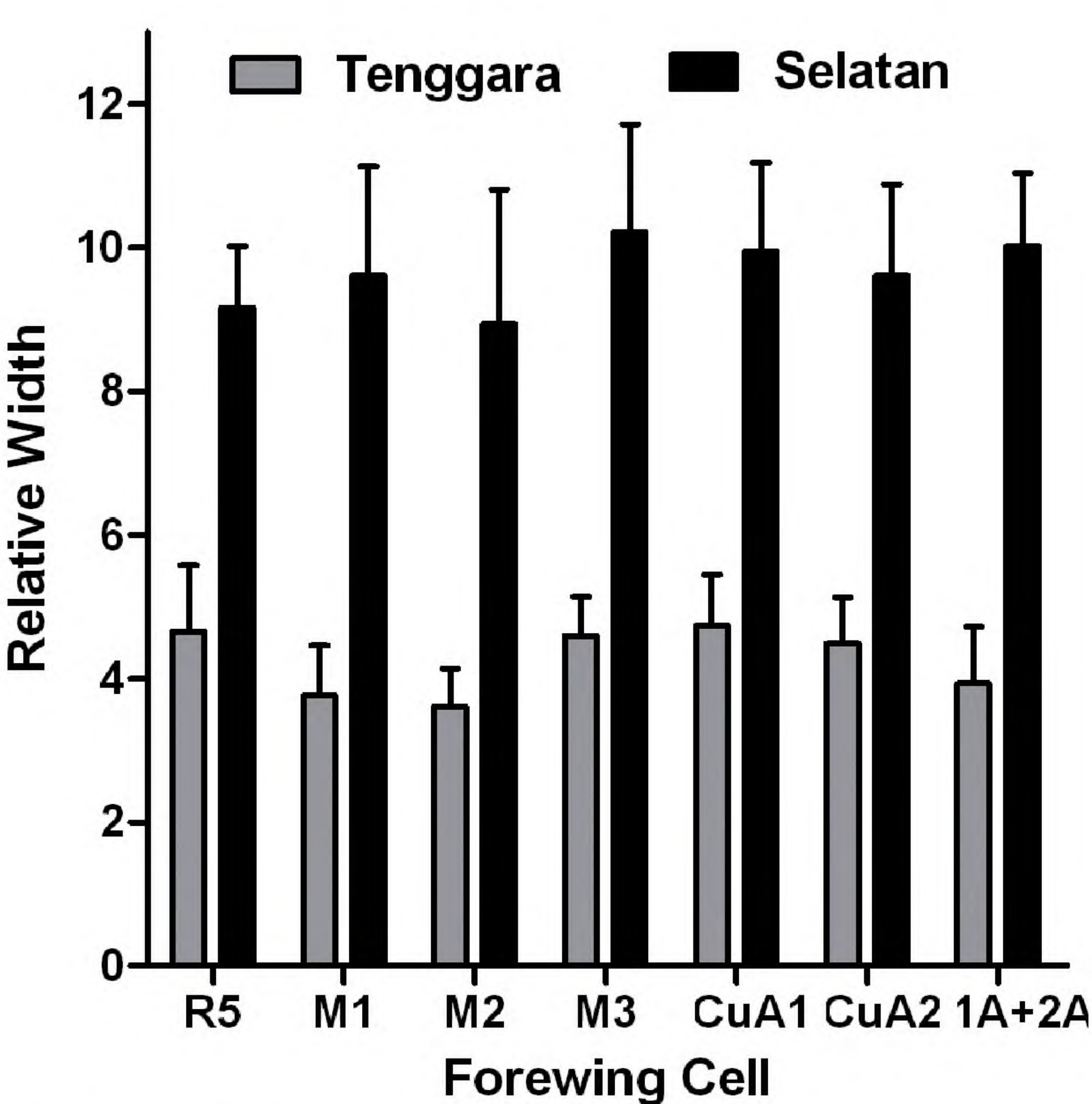


Figure 13. Relative width of the white median band in the different wing cells on the forewing upperside of *Cyrestis strigata* from Sulawesi Tenggara and Sulawesi Selatan. The relative band width is given as percentage of the forewing lengths. Measurements were each executed for both forewings and then means of the two values were calculated. These were used for calculating means and standard deviations obtained from 4 specimens of Sulawesi Tenggara (Kolaka) and 3 specimens from Sulawesi Selatan (Rantepao, Sumarorong).

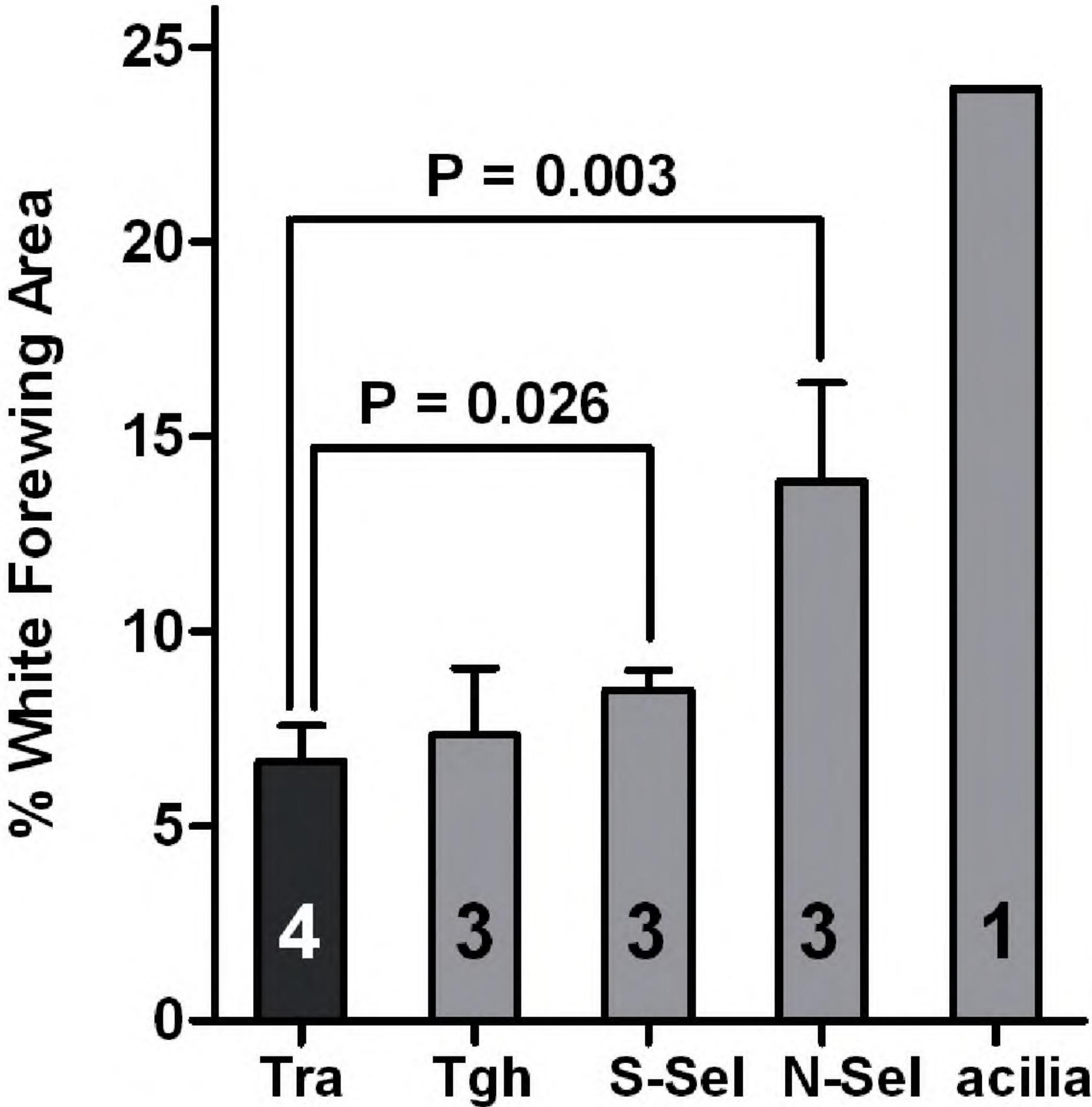


Figure 14. Area of the white median band on the forewings of *Cyrestis strigata*. The band area was determined on both forewings by means of the FIJI software and normalized of the total wing area. The means were used for further calculations concerning the different samples from Sulawesi Tenggara (Tra), Sulawesi Tengah (Tgh), southern (S-Sel) and northern Sulawesi Selatan (N-Sel). For comparison a representative specimen of *Cyrestis acilia* from Timika (Papua, Indonesia) was analyzed. The number of analyzed specimens is shown on the bars. Statistically significant differences as indicated.



14). Thus, the darkest forms of *C. strigata* occur in SE Sulawesi, similar to those from East Sulawesi.

***Cyrestis paulinus* Felder et Felder, 1860**

The species of the *Cyrestis* subgenus *Apsithra* Moore, 1899 (= *cocles* group) of the Sulawesi region are under current revision (Roos, in preparation). There are no published records of *C. paulinus* from SE Sulawesi although the distribution map of Tsukada et al. (1985) depicts the entire eastern parts of Sulawesi from the south to the north as distribution area for *C. paulinus mantilis* Staudinger, 1886. My own investigations have shown, however, that SE Sulawesi is not inhabited by ssp. *mantilis* but by ssp. *kransi* Jurriaanse et Lindemans, 1920, which has been described from the island Wowoni and is also known from Buton. The following locations and data can be given for *C. paulinus kransi* in SE Sulawesi: Porabua in March 2009, 2011 and 2013; Konawendepiha in March 2013; Uete in March 2011. The occurrence of ssp. *kransi* both in SE Sulawesi and its southern offshore islands underlines once more the faunistic relationship between these regions. To the contrary, the islands Peleng and Mangole (Sula Islands) off East Sulawesi bear the ssp. *kuehni* Röber, 1886 and ssp. *seneca* Wallace, 1869, respectively, while ssp. *mantilis* occurs on mainland East Sulawesi. It is not known whether there are contact zones or overlapping areas for *mantilis* and *kransi* in the northern parts of Sulawesi Tenggara. Furthermore, it is questionable whether the four different subspecies, i.e. *mantilis*, *kuehni*, *kransi* and *seneca* belong to one and the same species, *C. paulinus*. The different subspecies occurring in the Sulawesi region and further two, ssp. *gilolensis* Lathy, 1904 from Seram and ssp. *waigeuensis* Fruhstorfer, 1900 from Waigeo of the Papuan region are shown on plate 90 figs 1-16) for comparison. Clearly, the south-eastern ssp. *kransi* constitutes the *paulinus*-subspecies in which the dark wing pattern elements are most strongly broadened, although the intensity of the brown colour may be stronger in other subspecies. As the whole group is under revision detailed analyses are not presented here but the Figures on Plate 90 undoubtedly demonstrate the large differences in wing colour intensity and also patterns between the relevant subspecies. Considerable variation in wing colouration is observed in *C. paulinus kransi* reminiscent somewhat of the dry and wet season form of *Cyrestis cocles* Fabricius, 1787. However, both brighter or darker specimens of ssp. *kransi* have been taken at the same time at the same

location.

***Lexias aeetes* Hewitson, 1861**

L. aeetes is an endemic species of the Sulawesi region. As well as on the main island, the species also occurs on adjacent islands such as Peleng, Buton and Wowoni from which subspecies have been described. The most obvious variation in the wing colour pattern concerns the hindwing upperside which largely lacks any light markings in the subspecies of the offshore islands and shows clear markings of varying extension in the subspecies described from Sulawesi proper. According to the current literature, the nominate subspecies occurs in North Sulawesi, ssp. *satellita* Jurriaanse et Lindemans, 1920 in Central Sulawesi and ssp. *phasiana* in South Sulawesi (Tsukada 1991; Vane-Wright & de Jong 2003). Although data are obviously missing, Tsukada (1991) includes SE Sulawesi in the range of ssp. *satellita*, while Vane-Wright & de Jong (2003) do not mention any subspecies from that part of the island. This is the state of prior knowledge. Analysis of specimens from SE Sulawesi and evaluation of literature data reveals that this current picture needs to be corrected.

Wing pattern analyses of specimens from different localities in SE Sulawesi, i.e. Moramo, Sambeani, Asinua and Porabua, show that these populations coincide with ssp. *butongensis* Tsukada, 1991, which has been described from Buton Island which is located to the South of Sulawesi Tenggara. This subspecies is characterized by the hindwing upperside which is nearly devoid of any colour pattern as in ssp. *rubellio* Fruhstorfer, 1898 from Peleng Island located in the Banggai Archipelago of East Sulawesi.

Thus, *Lexias aeetes* is an example of a species from the family Nymphalidae which tends to have darker wings in the southeast compared to other regions in Sulawesi. Reduction of light markings on the hindwing, which is obvious from figs 1-4 (Plate 91), is also true for the forewings as substantiated by a detailed quantitative analysis of the colour pattern. This is exemplified by quantifying the area of four selected white patches on the forewing upperside. The white areas marked with a and b were determined in cells R5, M1, M2 and M3 of the left forewing of four specimens each from SE and Southwest Sulawesi (Fig. 15). For comparability, the areas of the patches were normalized on the total forewing area and given as percentage. It is noted that wing size and wing geometry do not differ between the populations (Table 2, next page).

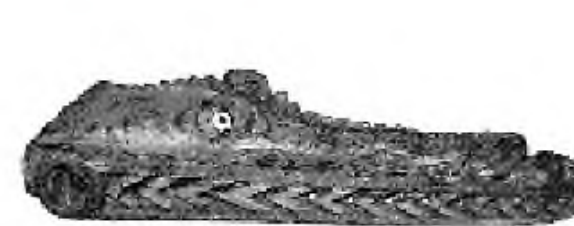


Table 2. Wing size and wing geometry of *Lexias aeetes* from Sulawesi Tenggara and Sulawesi Selatan.

Legends: The left forewings of four specimens each were analyzed. The parameters were quantified by means of photographs and the programm FIJI.

Parameter	Sulawesi Tenggara		Sulawesi Selatan	
	Mean	S.D.	Mean	S.D.
Wingspan (mm)	66.73	2.41	67.61	1.86
Forewing, length (mm)	38.77	0.83	38.82	0.97
Forewing, hindmargin (mm)	28,87	1.06	28.73	0.61
Forewing, height (mm)	24.03	0.67	25.01	0.78
- Length/Height (ratio)	1.61	0.06	1.55	0.05
Forewing, area (mm ²)	637	8	645	22

All five quantified patches appear generally smaller in specimens from SE Sulawesi compared to those from Southwest-Sulawesi although the differences are only significant for the pattern elements M2a, M3a and M3b (Fig. 16; Plate 91 figs 1-2). The P-values obtained by Student’s t-test are 0.029, 0.024 and 0.046, respectively. The total area of all measured patches is also significantly different between specimens from the two regions with P = 0.025. Means and standard deviations are (% sum of all patches area of total forewing area): 4.32 ± 0.80 and 5.62 ± 0.37 for specimens from SE- and Southwest Sulawesi, respectively.

The *L. aeetes* populations from SE Sulawesi can be assigned to the subspecies currently known as ssp. *butongensis* Tsukada, 1991 from Buton Island. However, this taxon is synonymous with *satellita* Jurriaanse et Lindemans, 1920, as will be outlined here. The latter subspecies has been described from Wowoni, a small island off the east coast of SE Sulawesi. Based on the original *satellita* description, the wing pattern clearly meets that of ssp. *butongensis* of Tsukada. A male of *satellita* from Palu figured by Tsukada (1991) does not match the characteristics of that subspecies but nearly coincides with ssp. *phasiana* Butler, 1870 from Southwest Sulawesi. This is also true for a male from Puncak Palopo figured by Casteleyn (2004) under the name *satellita*. According to the distribution map given by Tsukada (1991), ssp. *satellita* is said to occur in SE, East, Central and the northern parts of Southwest Sulawesi, up to the Palu Valley in the north, omitting, however, the type-locality Wowoni Island. The latter island is located just north of Buton. The current nomenclatorial and distribution status can be summarized as follows:

***Lexias aeetes* Hewitson, 1861 *satellita* Jurriaanse et Lindemans, 1920**
= ssp. *butongensis* Tsukada, 1991 **syn. nov.**

The distribution area of subspecies *satellita* covers the islands Buton, Kabaena and Wowoni and SE Sulawesi (Tsukada 1991; Jurriaanse & Lindemans 1920; Roos, this paper). The northern distribution limits of *satellita* are not known and it is also not clear whether or how far it penetrates into the eastern peninsula of Sulawesi, there eventually meeting ssp. *rubellio* Fruhstorfer, 1898 which also has largely reduced hindwing markings. The following locations and data for *L. aeetes* in SE Sulawesi can be given: Sambeani, 27.II.1999, Asinua, 14.X.2002, Porabua, 19.X.2005 / 18.III.2013, Silui, 14.III.2013 / 16.III.2015; Moramo, 03.IV.2009; Kendari, 26.III.2015.

***Neptis ida* Moore, 1858**

There is substantial wing pattern variability in *Neptis ida* within the Sulawesi region. As already stated by Vane-Wright & de Jong (2003), there is confusion about the subspecific taxonomy of the species and in the assignment of populations from different areas to described subspecies. According to Tsukada et al. (1985) *Neptis ida* is represented on both southern peninsulae of Sulawesi by the ssp. *sphaerica* Fruhstorfer, 1907. However, my own material shows that the populations of Southwest and SE Sulawesi clearly differ in their wing markings (Plate 91 figs 5-10). Additionally, *sphaerica* is introduced by Fruhstorfer (1907) as an infra-subspecific taxon and is thus not available as valid name (Eliot 1969).

The populations of *N. ida* from SE Sulawesi are characterized by darkened wing markings and thus follow the proposed darkening trend. To objectify this observation, wing pattern elements of the forewing upperside were analyzed in a verifiable way which can be applied for future comparative studies of further populations. The mean colour intensity was determined in equally sized rectangles placed within the white/grey pattern elements of



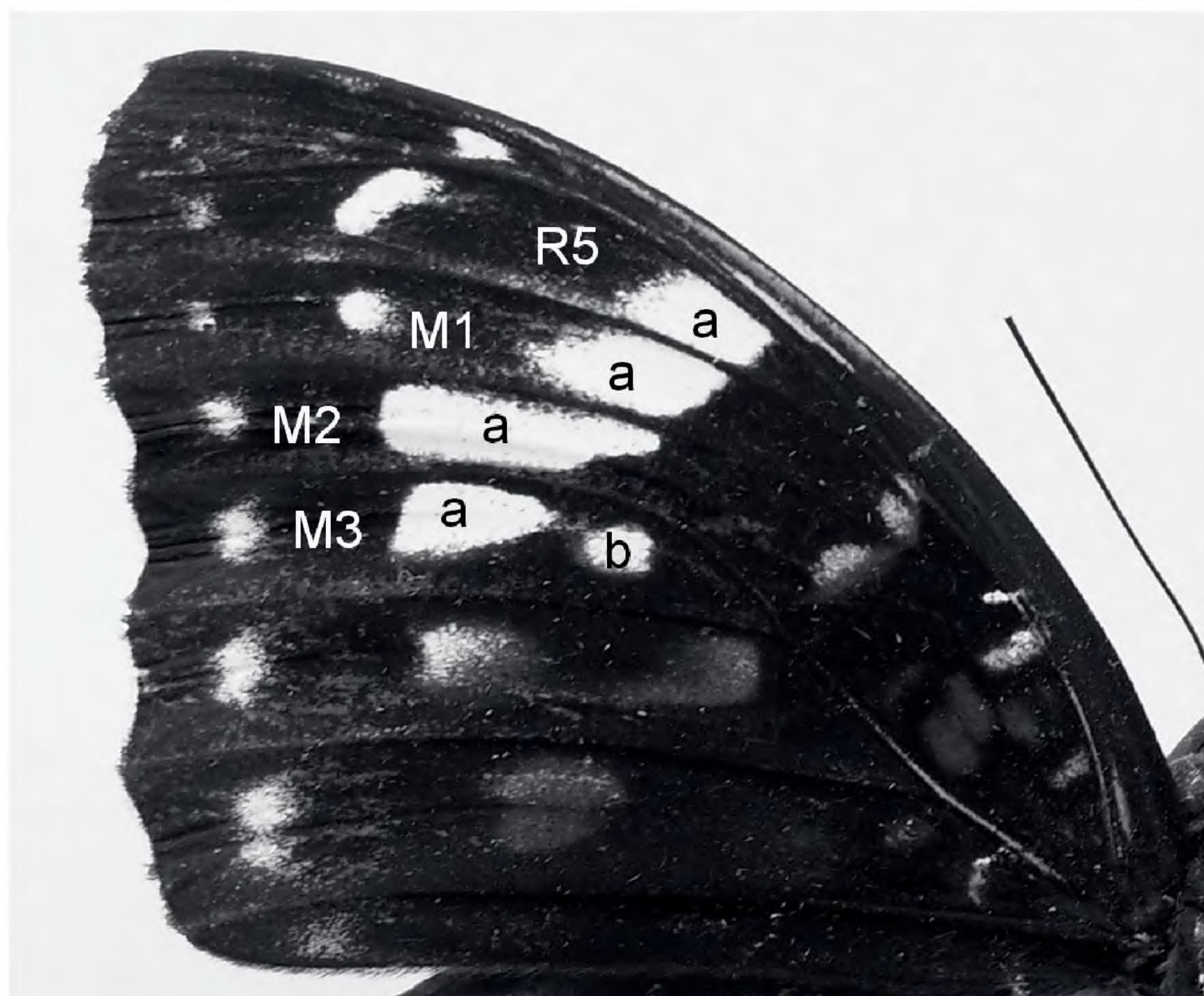


Figure 15. Quantification of wing pattern elements of *Lexias aeetes* Hewitson, 1861. Left: Forewing showing the areas used for quantitative analysis.

the forewing (F1, F2) and hindwing (H1 to H5) (Fig. 17). The patch in hindwing cell M2 is divided into two areas displaying different intensities marked with H3a and H3b. For comparison a specimen of *N. ida* from Sulawesi Selatan is shown in Figure 18. The intensity was also determined for a dark coloured area in forewing cell Cu1 as control.

A comparison of the patch intensities between *N. ida* specimens from Sulawesi Selatan and S. Tenggara shows that on the forewing all the patches are generally darker in the former. On the hindwing the darkening concerns the patches in wing cells R and M1 but not in cells Cu1 and Cu2. As already mentioned above, the cell in M2 is heterogenous. The results of the intensity measurements for specimens from the two Sulawesi provinces are shown in Figure 19. For this exploratory analysis only one specimen each was used and parameters were determined for both forewings. Finally, means were calculated and presented in a bar diagram. There are clear-cut intensity differences for the parameters F1, F2, H1, H2 and H3a while intensities are similar for H3b, H4 and H5 which may serve as a good control for the measurements. Out of the complete set of parameters three were selected for further studies with extended sample sizes. Intensities for F2, H2 and H4 (constant) were determined on both left and right wings for 9 specimens each from Sulawesi Tenggara and Sulawesi Selatan (Fig. 20). Characters F2 and H2 differ significantly between specimens from the two provinces with $P < 0.001$ in contrast to H4 ($P = 0.156$, not significant). By the described quantitative method, the darkening trend in *N. ida* from SE Sulawesi can be clearly demonstrated.

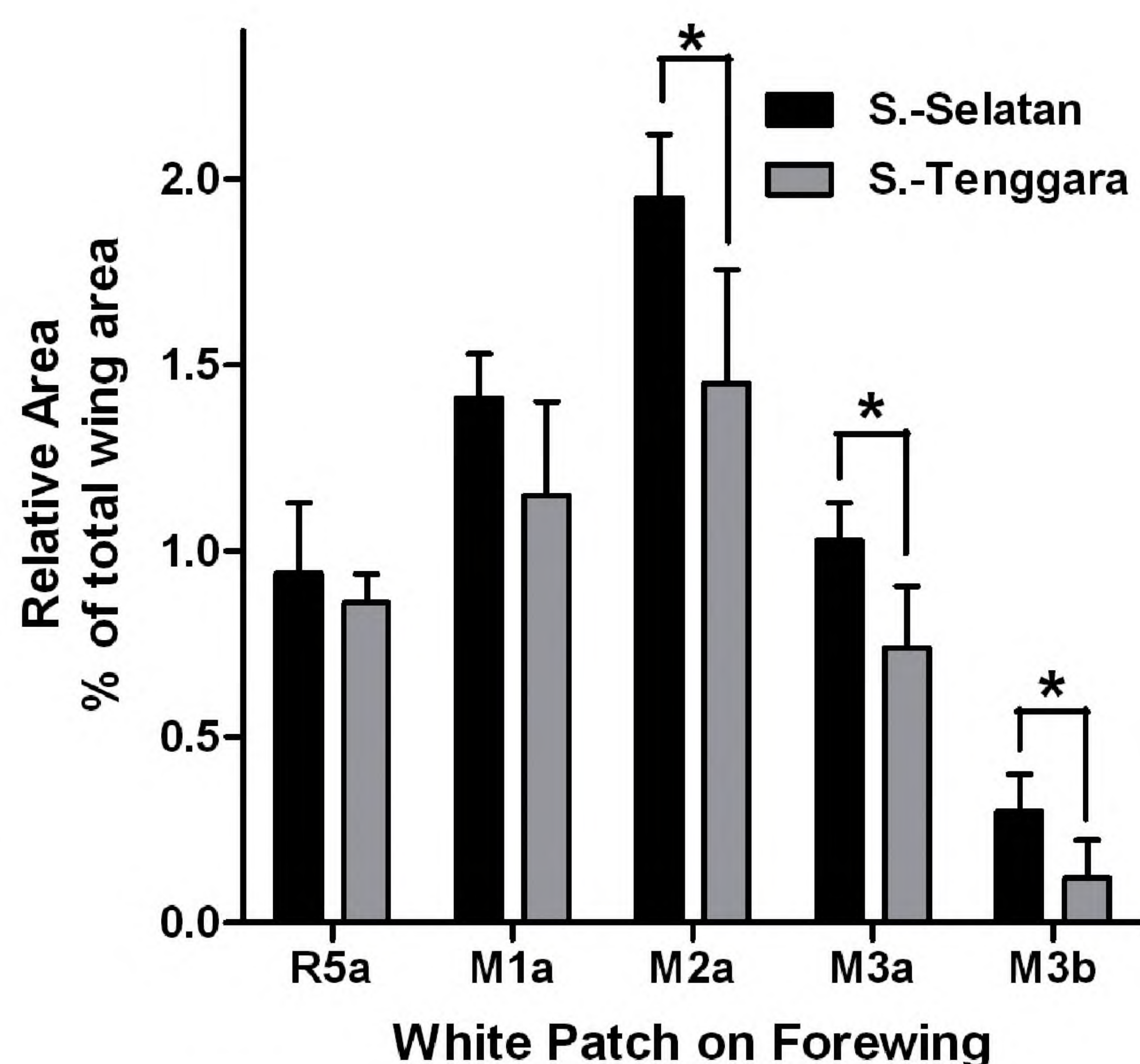


Figure 16. Bar-diagram showing the relative areas of the white patches (see Fig. 15) as a percentage of the total wing area for *Lexias aeetes* specimens from Sulawesi Selatan ($n = 4$) and Sulawesi Tenggara ($n = 4$). The areas were quantified on the left forewing of each specimen, using the FIJI software. The analyzed specimens originate from the following locations: Bantimurung (Sulawesi Selatan), Moramo, Porabua, Sambeani, Asenua (Sulawesi Tenggara). Significantly different values are marked with an asterisk (see text).

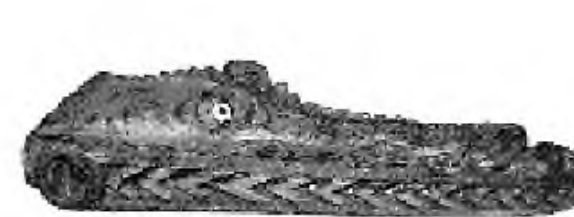
Besides the decrease in intensity, the white/grey patches in southeastern *N. ida* are also smaller than in specimens from Sulawesi Selatan (results not shown) thus additionally aggravating the darkening effect.

The current investigations shed some light on the confusing treatment of the infraspecific taxonomy of *N. ida*. However, populations from more subregions in Sulawesi have to be analyzed quantitatively to come to a final sound conclusion. Based on the above data the populations of SE Sulawesi are tentatively assigned to ssp. *carbonespersa* Martin, 1924.

There are more butterfly species or subspecies in SE Sulawesi showing the wing pattern darkening trend but they have not all been analyzed in detail. For a final proof relevant pattern elements have to be identified for each species and methods for their quantitative analyses have to be defined. For example, *Cepora timnatha* Hewitson, 1862 (Pieridae) and *Polyura cognata* Vollenhoven, 1861 (Nymphalidae) are prospective candidates.

Sulawesian butterfly species missing from Sulawesi Tenggara

In this last section, selected butterfly species will be listed which have not yet been reported from



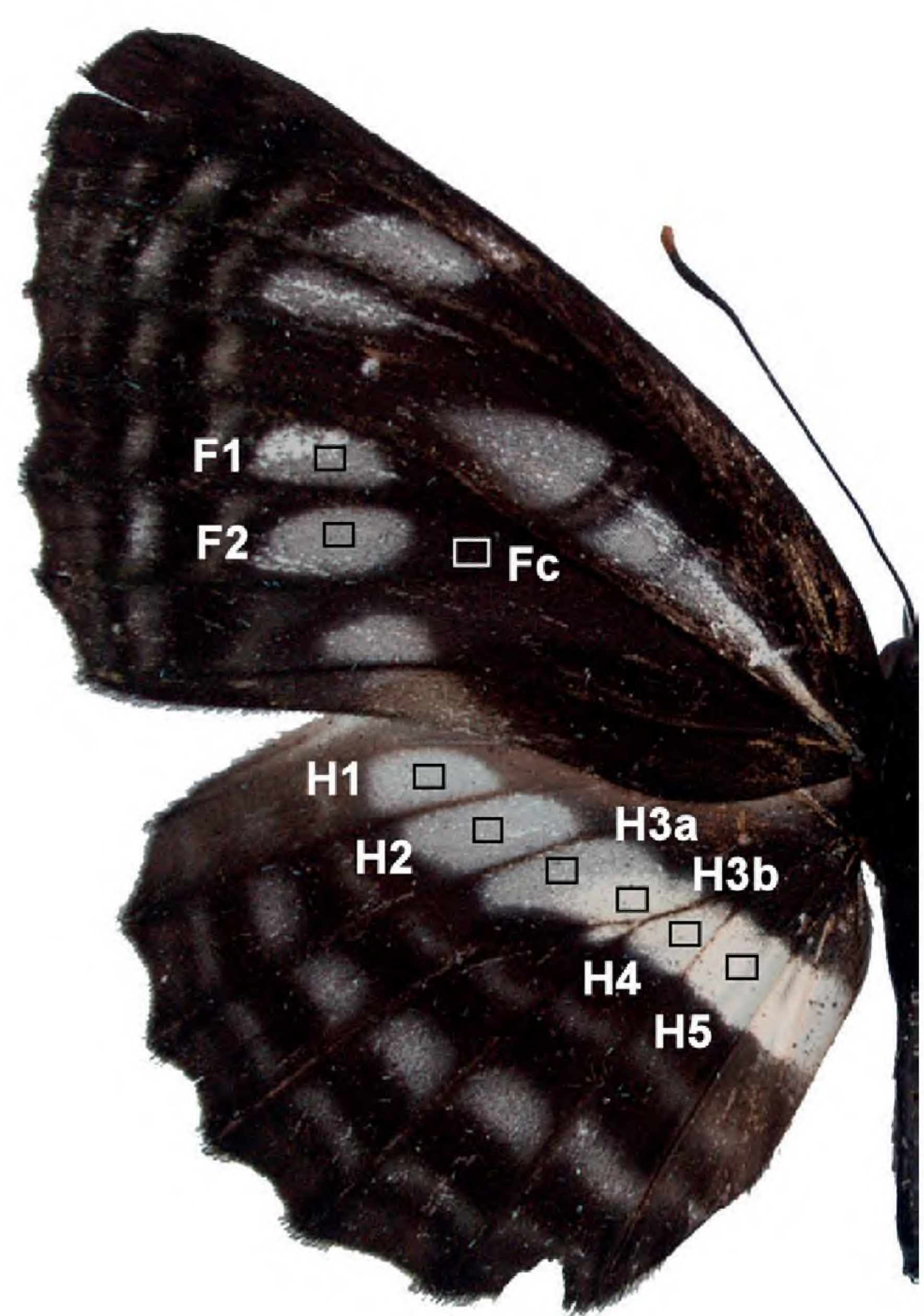


Figure 17. Areas on the wings of *Neptis ida* Moore, 1858 which were used for intensity measurements using FIJI-software. Specimen from Sulawesi Tenggara showing the transition in intensity of the hindwing median band from H3a to H3b in wing cell M2.



Figure 18. Specimen of *Neptis ida* from Sulawesi Selatan for comparison showing the uniformity in the intensity of the white median band on the hindwing which is different in specimens from Sulawesi Tenggara (Fig. 17).

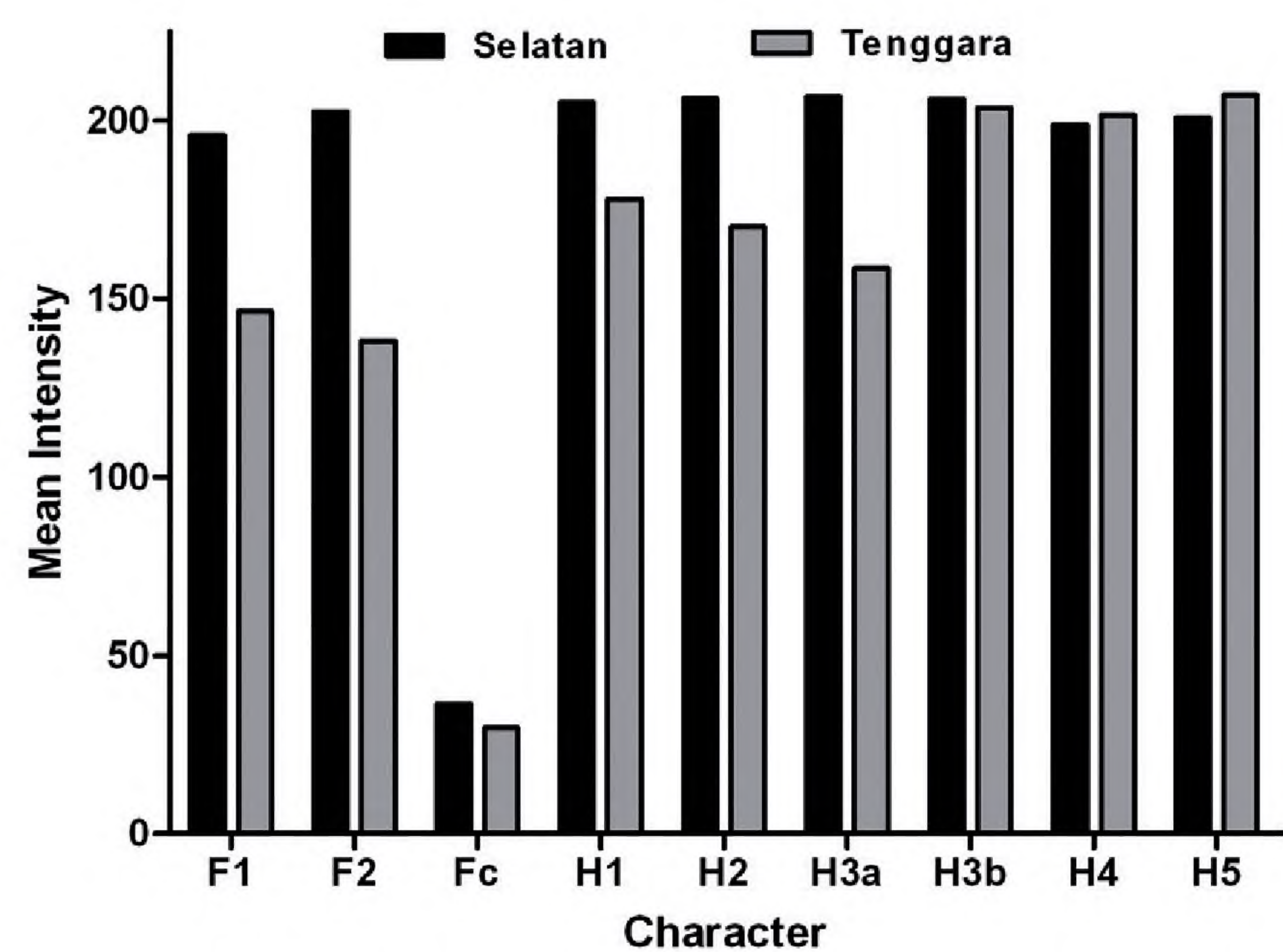


Figure 19. Comparative quantitative analysis of the wing pattern of *Neptis ida* from Sulawesi Tenggara and Sulawesi Selatan. The intensities of the median band in the different wing cells were quantified in equally sized rectangles by FIJI. Only one representative specimen from each region was analyzed. Values are means of the measurements on the left and the right wings.

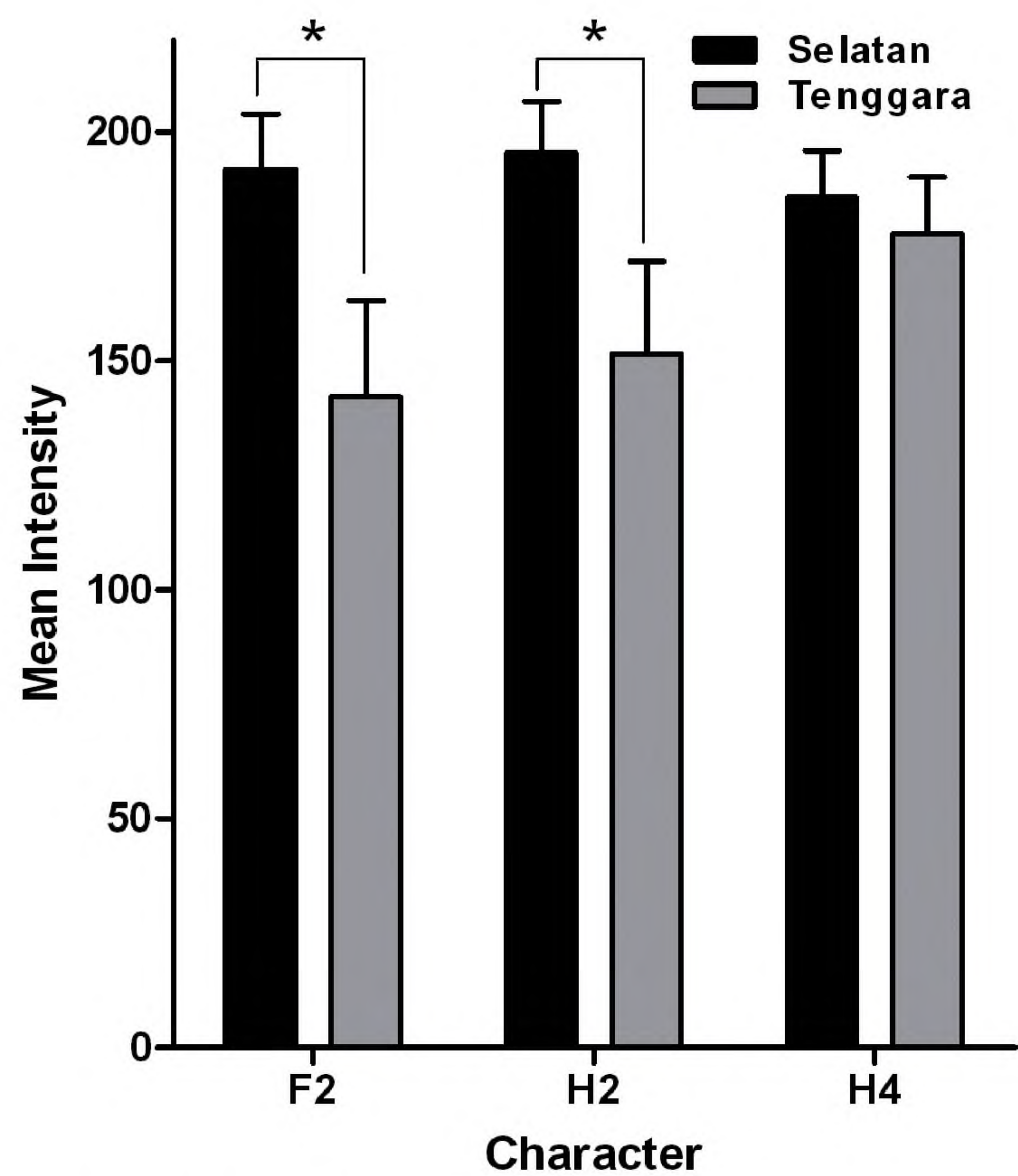


Figure 20. Intensities of the median band for characters F2, H2 and H4 (see fig 17) of *Neptis ida* from Sulawesi Tenggara and Sulawesi Selatan. From each region, 9 specimens were analyzed. Statistically significant differences are marked with an asterisk ($P < 0.001$).

SE Sulawesi, but which occur in other parts of the island as indicated. This concerns species which I assume are absent from this region – of course, a final proof cannot be given. It is noted that only examples are given in the following table (Parts of Sulawesi: C – Central; E – East; N – North; S – South).

Papilionidae

- Atrophaneura dixonii* Grose-Smith, 1901 C N
- Atrophaneura kuehni* Honrath, 1886 C E N
- Losaria palu* Martin, 1912 C
- Papilio jordani* Fruhstorfer, 1906 N
- Graphium euphrates* Felder et Felder, 1862 S



Pieridae

Delias Hübner, 1819

There are ten species of the genus in the Sulawesi region (Vane-Wright & de Jong 2003). However, there are no definitive reports of any of them for mainland Sulawesi Tenggara. Not a single *Delias* is listed by Jurriaanse and Lindemans (1920). Although the distribution maps for *D. kuehni* Honrath, 1886, *D. rosenbergi* Vollenhoven, 1865 and *D. zebuda* Hewitson, 1862 in Yata and Morishita (1985) at least partially cover SE Sulawesi, there is not any proof for their occurrence in that region; not a single definite locality is given. Also Martin (1920) does not report them for SE Sulawesi. However, *D. rosenbergi* is likely to occur in SE Sulawesi as there exists a subspecies, ssp. *munaensis* Nakano, 1988, on the islands Muna and Buton. As is often the case, taxa from these islands are also present on mainland SE Sulawesi. Furthermore, Yagishita et al. (1993) and also Vane-Wright and de Jong (2003) refer *D. rosenbergi* from SE Sulawesi.

Eurema irena Corbet, Pendlebury, 1932 C

Ixias piepersi Snellen, 1878 S

Ixias paluensis Martin, 1914 C

Cepora fora Fruhstorfer, 1897 C N S

Nymphalidae, Satyrinae

Lohora dinon Hewitson, 1864 S

Lohora anna Vane-Wright et Fermon, 2003 C

Lohora deianirina Fruhstorfer, 1897 C N

Lohora deianira Hewitson, 1862 N

Lohora imitatrix Martin, 1929 C

Lohora erna Fruhstorfer, 1898 S

Lohora tanuki Tsukada et Nishiyama, 1979 C E

Nirvanopsis hypnus Tsukada et Nishiyama, 1979 C E

Acrophthalmia windorum Miller et Miller, 1978 C N

Nymphalidae, Danainae

Parantica sulewattan Fruhstorfer, 1896 S

Parantica kuekenthali Pagenstecher, 1896 N

Nymphalidae, Charaxinae

Charaxes mars Staudinger, 1885 C N S

Nymphalidae, Nymphalinae

Cyrestis heracles Staudinger, 1896 C N

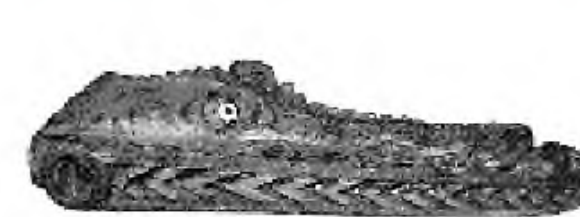
Discussion and concluding remarks

The butterfly fauna of Sulawesi has been studied by many entomologists with great interest. However, large areas such as SE and East Sulawesi have been largely excluded from the investigations, although the off-shore islands in these regions such as Buton, Muna and the Banggai archipelago attracted some interest. For understanding the zoogeography and evolution of the Sulawesi butterfly fauna, data from the neglected areas are needed. From their geological history, these two parts of Sulawesi are distinct as they are of different tectonic origin compared to West and North Sulawesi. The western and eastern block originate from different parts of Gondwanaland and were separated from each other for a long time period of about 200 Ma. The collision of both blocks is dated in the middle miocene, about 15 million years ago (Audley-Charles 1987). A third geological province of the Sulawesi region, recognized by Sukanto & Simandjuntak (1983), is the archipelago east of Sulawesi, i.e. the Banggai and Sula Islands. The islands south of SE Sulawesi, such as Buton and Muna, drifted separately from the eastern Sulawesi block as micro-continental blocks (Moss & Wilson 1998). The geological provinces, however, do not coincide with biogeographical entities. Based on the above presented results, the butterfly fauna of SE Sulawesi appears to be more closely related to that of the islands Buton and Muna than to neighbouring fauna of East Sulawesi. This is underlined by the common occurrence of specific taxa such as *Parthenos sylvia ornatrix*, *Cyrestis paulinus kransi* and *Lohora umbrosa* which are not found in other parts of Sulawesi. In addition, the trend for wing pattern darkening in certain butterflies is paralleled for these islands and SE Sulawesi. In terms of butterfly distribution it is therefore suggested to define parts of SE Sulawesi together with its southern off-shore islands a discrete zoogeographic entity within the Sulawesi region and to distinguish it from East Sulawesi.

The question arises now where there are the northern limits of this zoogeographic entity (Fig. 21). For answering this question, studies on the distribution of the following pairs of taxa or species will be helpful (most northern localities known so far for the first mentioned southeastern taxon are given in parenthesis):

Parthenos sylvia ornatrix (Uete) vs. *Parthenos sylvia salentia*.

Cyrestis paulinus kransi (Konawendepiha) vs.



Cyrestis paulinus mantilis.

Zethera incerta tenggara (Andamau) vs. *Zethera incerta incerta*.

It cannot be excluded that the three aforementioned subspecies from SE Sulawesi constitute species distinct from *P. sylvia*, *C. paulinus* and *Z. incerta*, respectively.

Lohora umbrosa vs. *Lohora decipiens* (Porabua). These are probably sister species (preliminary morphological and molecular data).

Cirrochroa recondita (Sambeani). A vicariant partner is not defined. The most related species is presumably *Cirrochroa eremita* Tsukada, 1985 which is known so far, however, only from North Sulawesi.

Unfortunately, there are no faunistic data on butterflies from the relevant regions which may include the borders or contact zones of the mentioned species or subspecies. Large areas of northern SE Sulawesi are obviously not explored entomologically, such as the Meluhu, Abuki, Matarombeo and Tangkelemboke Mountains. As a first working hypothesis, the Lawanopo fault which runs from the Gulf of Bone in the north across SE Sulawesi to close of Kendari on the east coast is selected as boundary so that the south-eastern zoogeographic entity can be defined as shown in Fig. 22. The northern demarcation in SE Sulawesi of the area is similar to that used by van Baaloooy (1987) for a plant geographical analysis. The area largely coincides with the central Sulawesi metamorphic belt (Hamilton 1979) but includes Buton, in addition. The Lawanopo fault system has been described in detail by Natawidjaja and Daryono (2015) so that the location of the prospective zoogeographical boundary can be easily retraced.

Another question concerns the evolutionary origin of the species of the southeast sub-region. For this, either the western or eastern block has to be considered as origin as the micro-continental blocks which later formed the off-shore islands could not have served as rafts carrying terrestrial species or biota from the Australian Plate because they were submerged for longer periods (Moss & Wilson 1998). On this background, the case of the Satyrine genus *Lohora* should be discussed here shortly. According to Kodandaramaiah et al. (2010) the genera *Lohora* and *Mycalesis* diverged about 24 Ma ago, which is before the collision of the western and eastern Sulawesi block. Species

splitting processes within the *Lohora* radiation can be dated back to 3 Ma concerning for example the divergence between *L. transiens* Fruhstorfer, 1908 and *L. ophthalmicus* Westwood, 1888. Independent development of *Lohora* on the eastern and western block is not probable. However, a decision from which block the dispersal and following radiation started cannot be answered based on available data. Stelbrink et al. (2012) discussed possible dispersal and vicariance scenarios for Sulawesi and came to the conclusion that most Sulawesi taxa originate from Asian ancestors and thus invaded via the western block. A phylogenetic analysis of the genus *Lohora* will probably help to answer the questions concerning the evolutionary history of the species and to explain current distribution patterns. Similar analyses have to be performed for all Sulawesi butterfly species. The evolutionary history of the different taxa of the *Cyrestis cocles* group within the Sulawesi region appears particularly interesting. An Australian origin of *C. paulinus kransi* cannot be excluded as invasion via dynamic land connections as discussed by Stelbrink et al. (2012) is conceivable.

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Figure 21. Where to locate the contact zones of related allopatric taxa occurring in SE Sulawesi (A) or in the North of it (B)? Examples: *Parthenos sylvia ornatrix* (A) and *P. sylvia salentia* (B); *Cyrestis paulinus kransi* (A) and *C. paulinus mantilis* (B); *Zethera incerta tenggara* (A) and *Z. incerta incerta* (B).



Figure 22. The south-eastern zoogeographical unit of Sulawesi (shaded in dark grey). The Lawanopo fault system is assumed as northern boundary. The islands Buton (B), Muna (M), Kabaena (K) and Wowoni (W) are included in the unit. The still further southeast located islands of the Tukang Besi Archipelago may also be added but were omitted here due to the lack of data.

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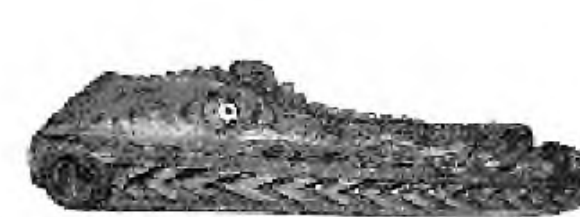
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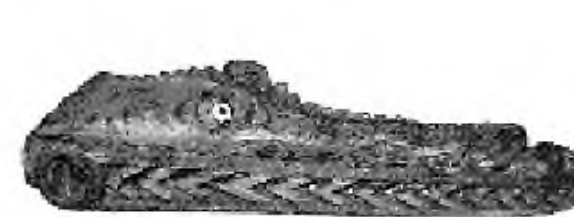
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Appendix

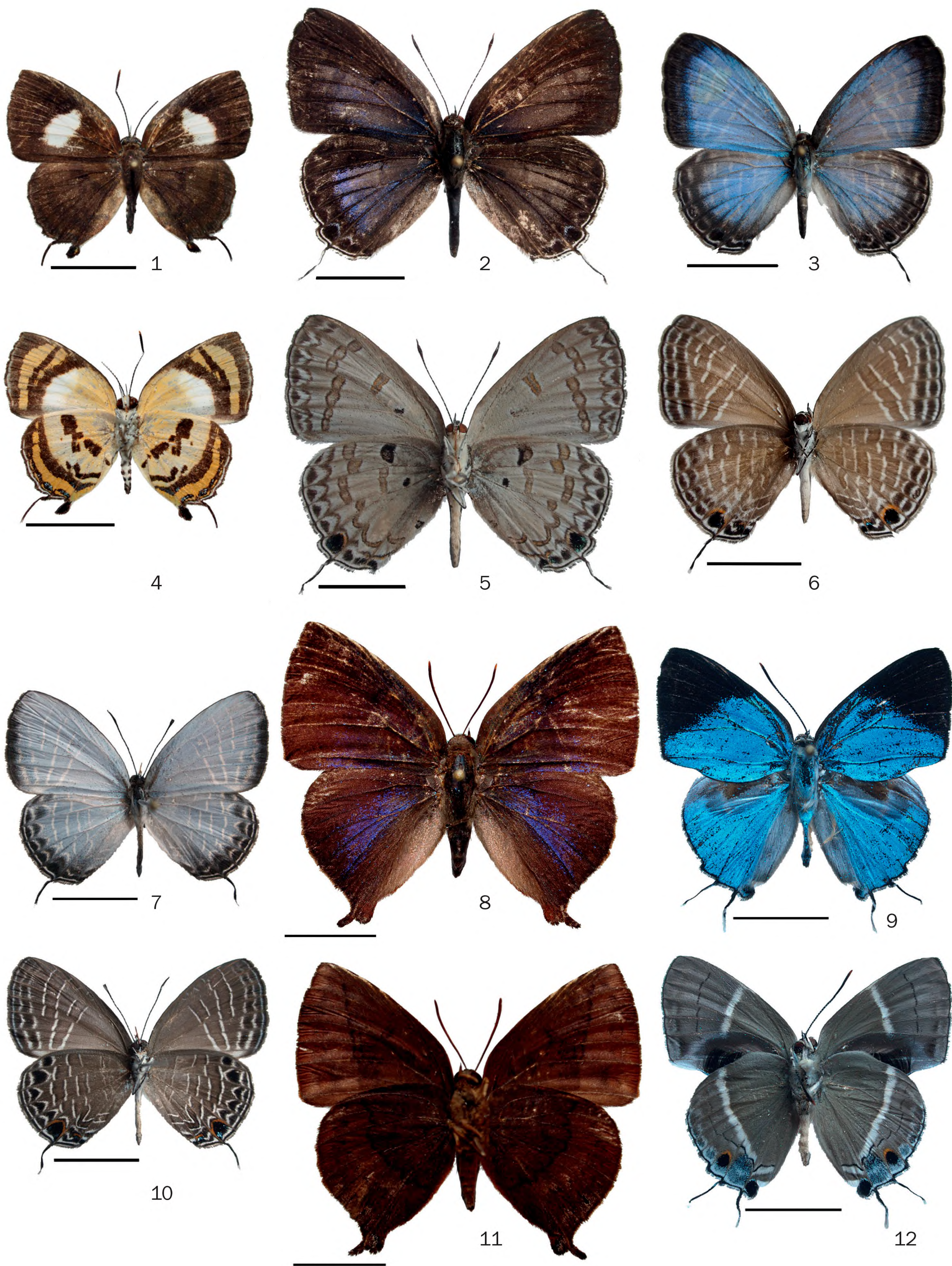
Table 3. List of localities including coordinates and altitudes.

Province / Locality	Latitude	Longitude	Altitude (m)
Sulawesi Tenggara			
Andamao	-3.699583	121.544417	140
Asenua	-3.7000	121.8000	138
Asolu	-3.738056	121.886944	60
Kendari	-3.945	122.4988889	150
Kolaka	-4.05	121.6	16
Kolaka, 20 km East of	-4.0421	121.709933	238
Konawendepiha	-3.714858	121.562856	115
Lasada	-3.716389	121.842778	156
Moramo	-4.1500	122.6333	148
Porabua	-3.734461	121.597403	110
Sambeani	-3.7579	121.9268	139
Silui	-3.736717	121.591133	270
Uete	-3.742853	121.624947	105
Sulawesi Selatan			
Bantimurung	-4.8433333	119.72	
Sumarorong	-3.147967	119.305772	920
Sulawesi Tengah			
Koyoan, Dowiwi	-1.04265	122.730483	211
Luwuk	-0.9333	122.7833	70



Plate 85

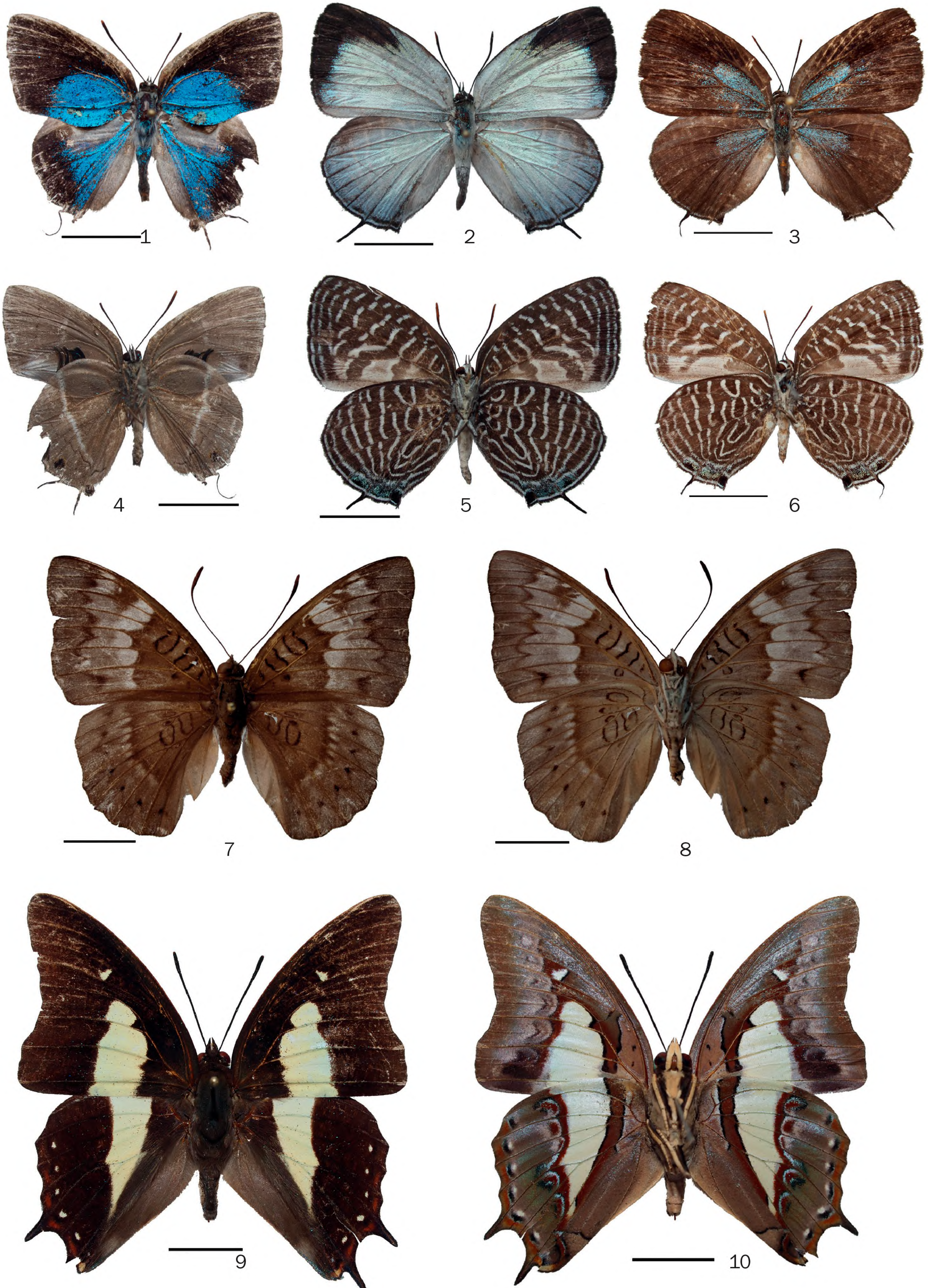
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Figures 1-12. Lycaenidae from Southeast Sulawesi with their upperside (rows 1 and 3) and underside (rows 2 and 4) wing patterns. 1, 4 – Female of *Deudorix loxias* (20 km East of Kolaka), wing span: 29,0 mm; 2, 5 – *Hypothecia honos* de Nicéville, 1898 (Konawendepiha, 17.03.2013); 3, 6 – Male of *Jamides latimargus* Snellen, 1878 (Konawendepiha, 17.03.2013); 7, 10 – *J. fractilinea* Tite, 1960 (20 km E of Kolaka, 31.03.2009); 8, 11 – Male of *Amblypodia narada* Horsfield, 1829 (Porabua, 12.03.2011); 9, 12 - *Dacalana anysis* Hewitson, 1865 (Konawendepiha, 10.03.2011) [scale bars 10 mm].

Plate 86

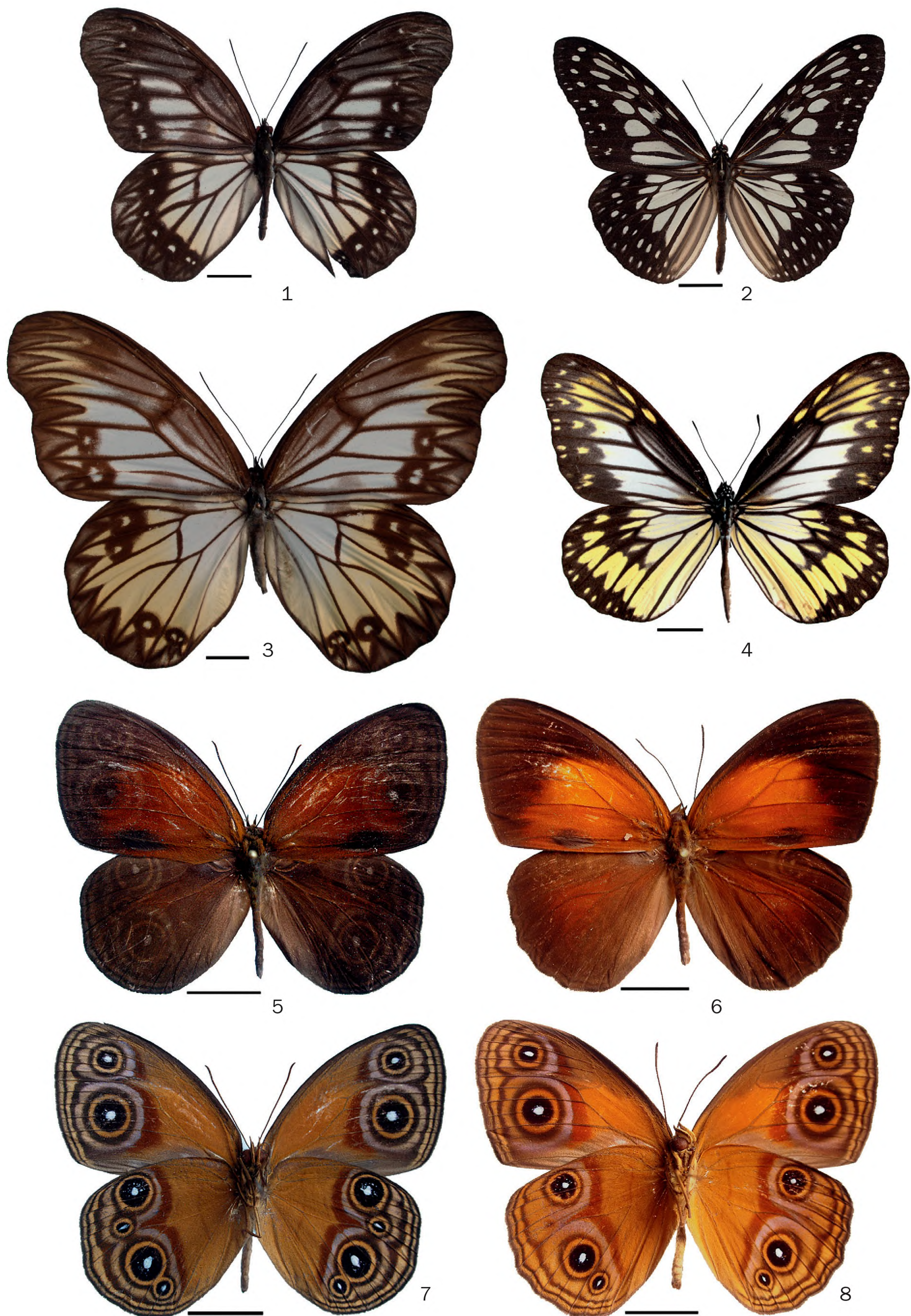
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Figures 1-10. Particular butterflies from Southeast Sulawesi (upperside and underside. 1, 4 – *Dacalana anysides* Röber, 1887 (Porabua, 20.03.2013); 2, 5 – Male *Arhopala argentea* Staudinger, 1888 (20 km East of Kolaka, 20.03.2015); 3, 6 – Female *A. argentea* (20 km East of Kolaka, 22.03.2015); 7-8 – *Euthalia aconthea* Cramer, 1777 (20 km East of Kolaka, 16.10.2002), upperside (left) and underside (right); 9-10 – *Polyura attalus* Felder et Felder, 1867 (Konaweandepiha, 06.03.2011), upperside (left) and underside (right) [scale bars 10 mm].

Plate 87

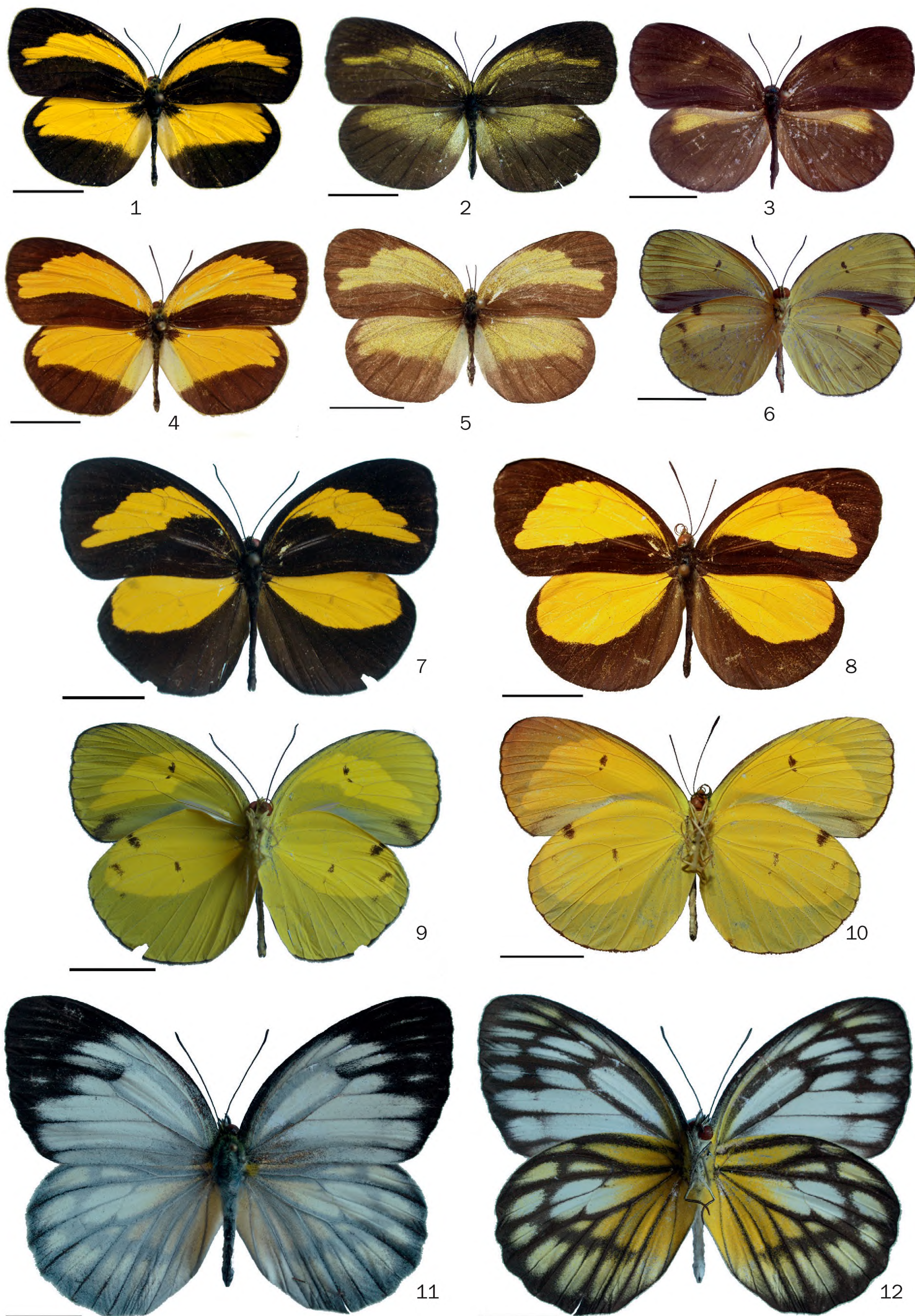
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Figures 1-8. Butterflies of Southeast Sulawesi. 1-4 – Subspecies of *Zethera incerta* Hewitson, 1861 and their prospective mimicry counterparts: 1 – *Z. incerta tenggara* Roos, 1992 (Sambeani, 02.03.1999); 2 – *Ideopsis juvena* Cramer, 1777 (Sambeani, 01.03.1999); 3 – *Z. incerta incerta* Hewitson, 1861 (Sulawesi); 4 – *I. vitrea* Blanchard, 1853 (Porabua, 24.03.2009); 5, 7 – Male of *Lohora umbrosa* Roos, 1997 (Porabua, 13.03.2011), upperside (5) and underside (7) wing pattern; 6, 8 – Male of *Lohora decipiens* Martin, 1929 for comparison (25 km E of Rantepao, 10.03.1986) [scale bars 10 mm].

Plate 88

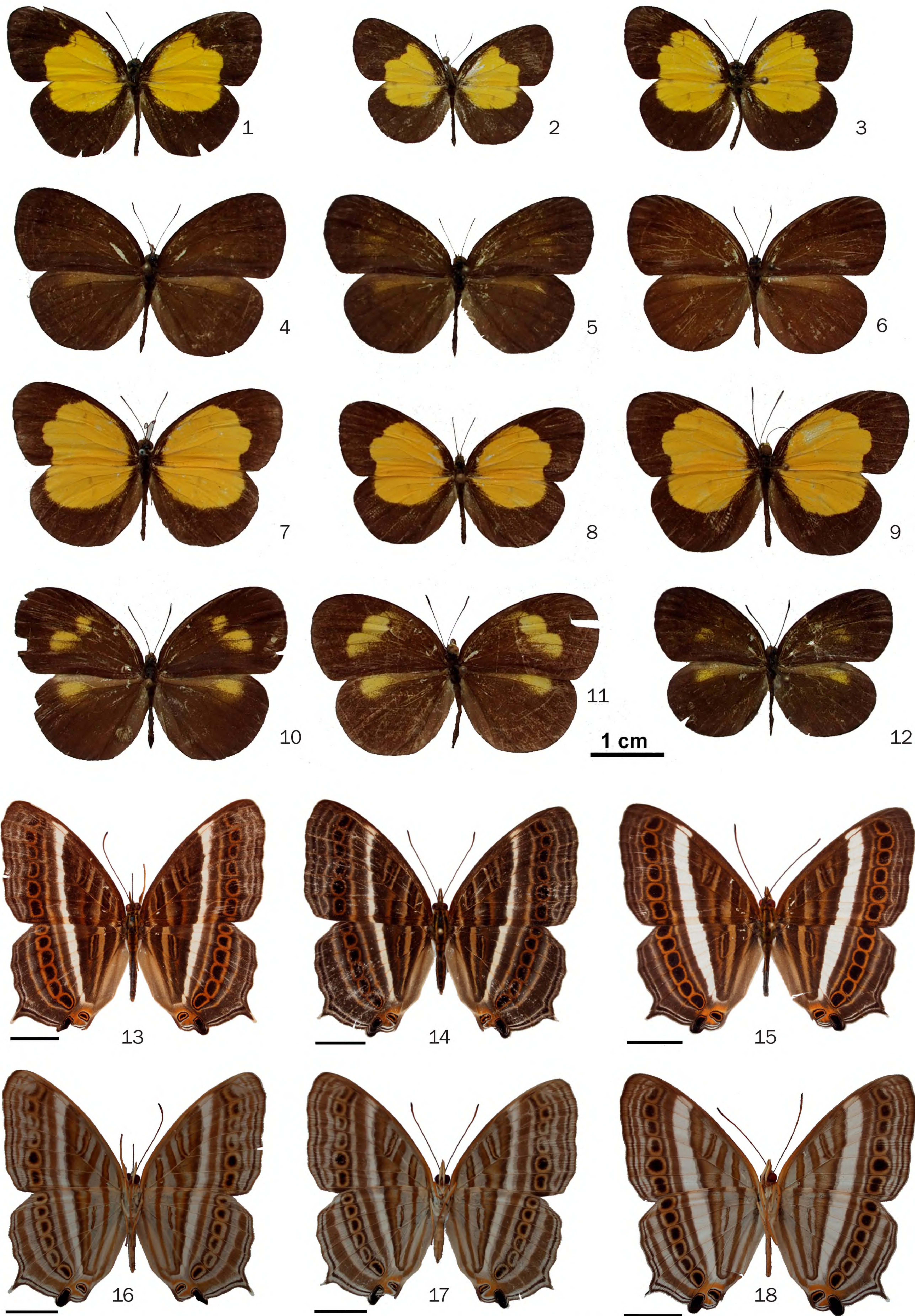
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Figures 1–12. *Eurema* from SE Sulawesi and their southwestern counterparts (1-10) and *Cepora eperia* from SE Sulawesi (11-12). 1 – Male *Eurema alitha* Felder et Felder, 1862 (SE–Sulawesi); 2 – Female of *E. alitha* (SE Sulawesi); 3 – Female *E. tominia* Vollenhoven, 1865 (SE Sulawesi), upperside; 4 – Male *E. alitha* (Southwest Sulawesi); 5 – ditto, female (Southwest Sulawesi); 6 – Underside of the female *E. tominia* shown in Fig. 3; 7-10 – Upperside (row 3) and underside (row 4) wing pattern of male *E. tominia*; 7, 9 – Male from Kolaka, SE Sulawesi. 8, 10 – Male from Sumarorong, SW Sulawesi; 11–12 – *Cepora eperia* Boisduval, 1836 (Porabua, 26.03.2009) [scale bars 10 mm].

Plate 89

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Figures 1-18. Butterflies of SE Sulawesi. 1-12 – *Eurema celebensis* Wallace, 1867: 1-3 – Males from Sulawesi Tenggara; 4-6 – Females from Sulawesi Tenggara; 7-9 – Males from Sulawesi Selatan; 10-11 – Females from Sulawesi Selatan; 12 – Female from Sulawesi Tengah; 13-15 – Uppersides of *Cyrestis strigata* from Sulawesi Tenggara and Sulawesi Selatan: 13 – Sulawesi Tenggara, Lasada, 03.03.1999; 14 – Sulawesi Tenggara, Kolaka, 22.03.2013; 15 – Sulawesi Selatan, Sumarorong, 14–18.03.1990; 16-18 – Respective underside wing patterns of figs 13-15 [scale bars 10 mm].

Plate 90

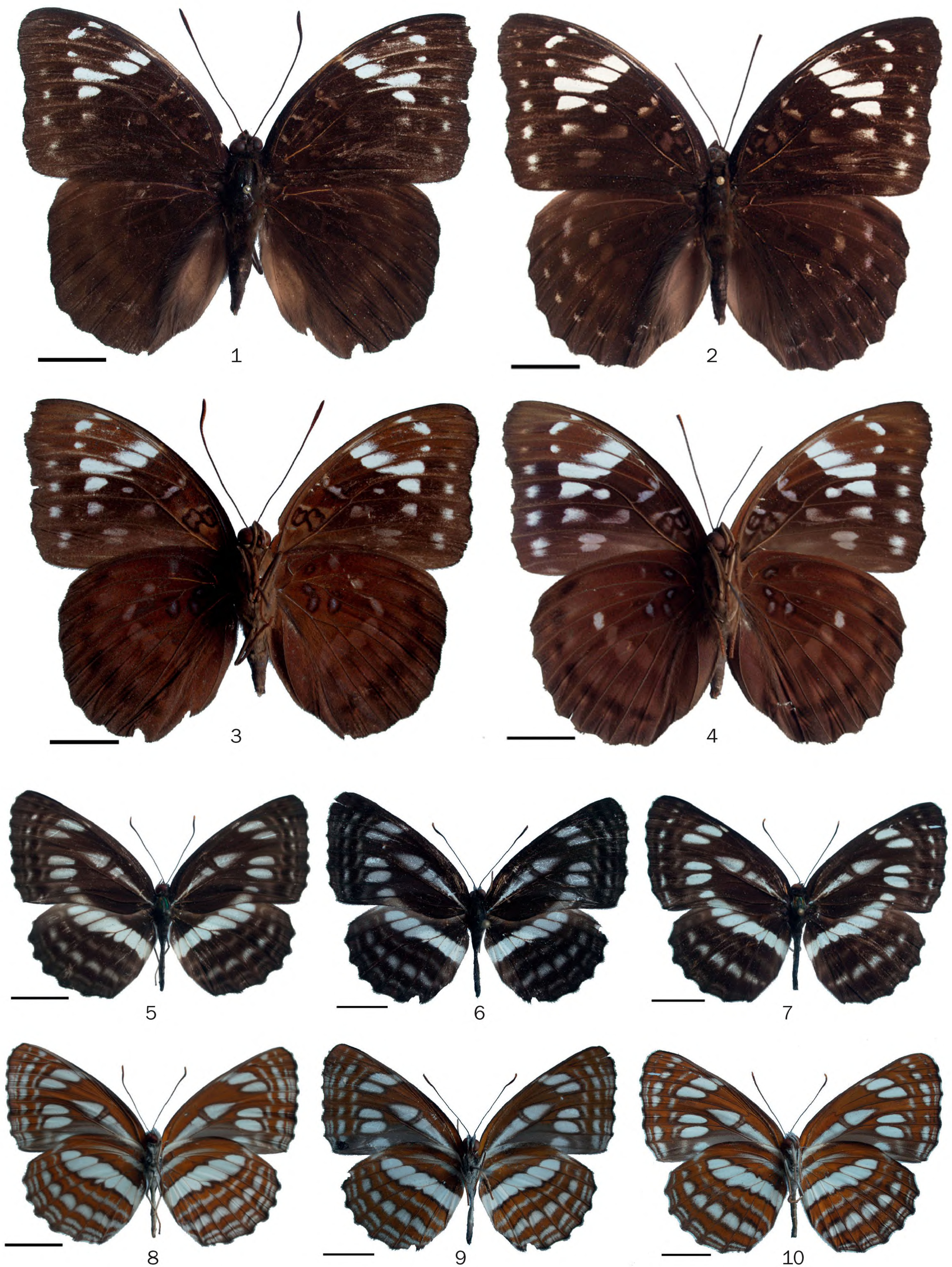
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Figures 1-16. Different subspecies of *Cyrestis paulinus* Felder et Felder, 1860. 1 – ssp. *kransi* Jurriaanse et Lindemans, 1920, SE Sulawesi; 2 – ssp. *mantilis* Staudinger, 1886, Sulawesi Tengah; 3-8 – Variability in ssp. *kransi*, SE Sulawesi; 9-10 – ssp. *mantilis*, Koyoan, East Sulawesi; 11 – ssp. *mantilis*, Toraut, North Sulawesi; 12 – ssp. *mantilis*, Palu, Central-Sulawesi; 13 – ssp. *kuehni* Röber, 1886, Peleng Island; 14 – ssp. *seneca* Wallace, 1869, Taliabu (Sula Islands); 15 – ssp. *gilolensis* Lathy, 1904, Seram (Maluku Islands); 16 – ssp. *waigeuensis* Fruhstorfer, 1900, Waigeo (Raja Ampat Archipelago) [scale bars 10 mm].

Plate 91

Roos, P.H.: Peculiarities of the butterfly fauna of South-East Sulawesi



Figures 1-10. Comparison of *Lexias aeetes* Hewitson, 1861 and *Neptis ida* Moore, 1858 from Southeast and Southwest Sulawesi. 1-4 – *Lexias aeetes*: 1-2 – Male from SE Sulawesi, upperside (first row) and underside (second row); 3-4 – Male from Southwest Sulawesi, upperside (first row) and underside (second row); 5-7 – Uppersides of *Neptis ida*: 5 – Sambeani; 6 – Porabua; 7 – Sumarorong (Sulawesi Selatan); 8-10 – Respective underside wing patterns of figs 5-7 [scale bars 10 mm].